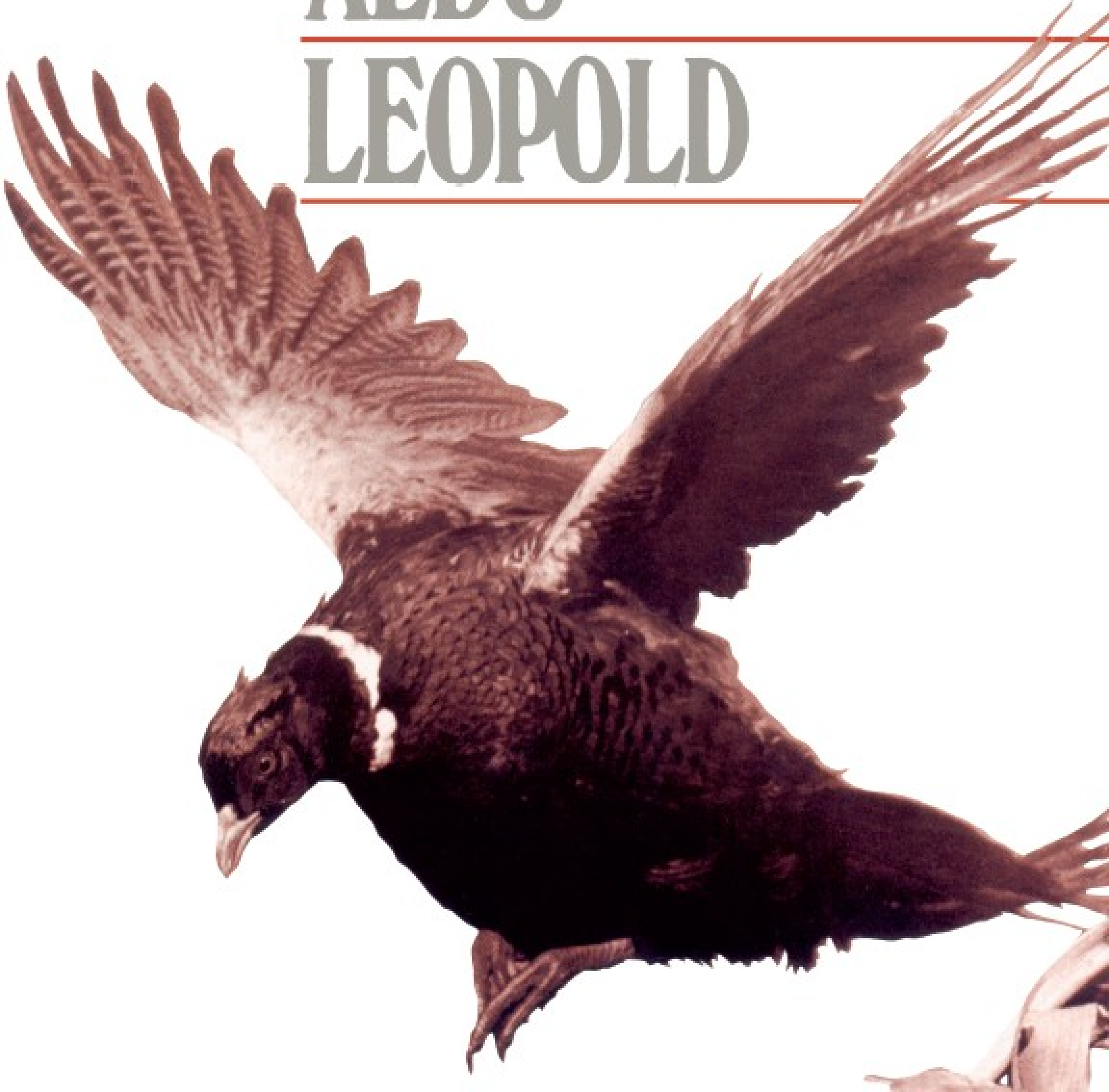
GAME MANAGEMENT

ALDO LEOPOLD



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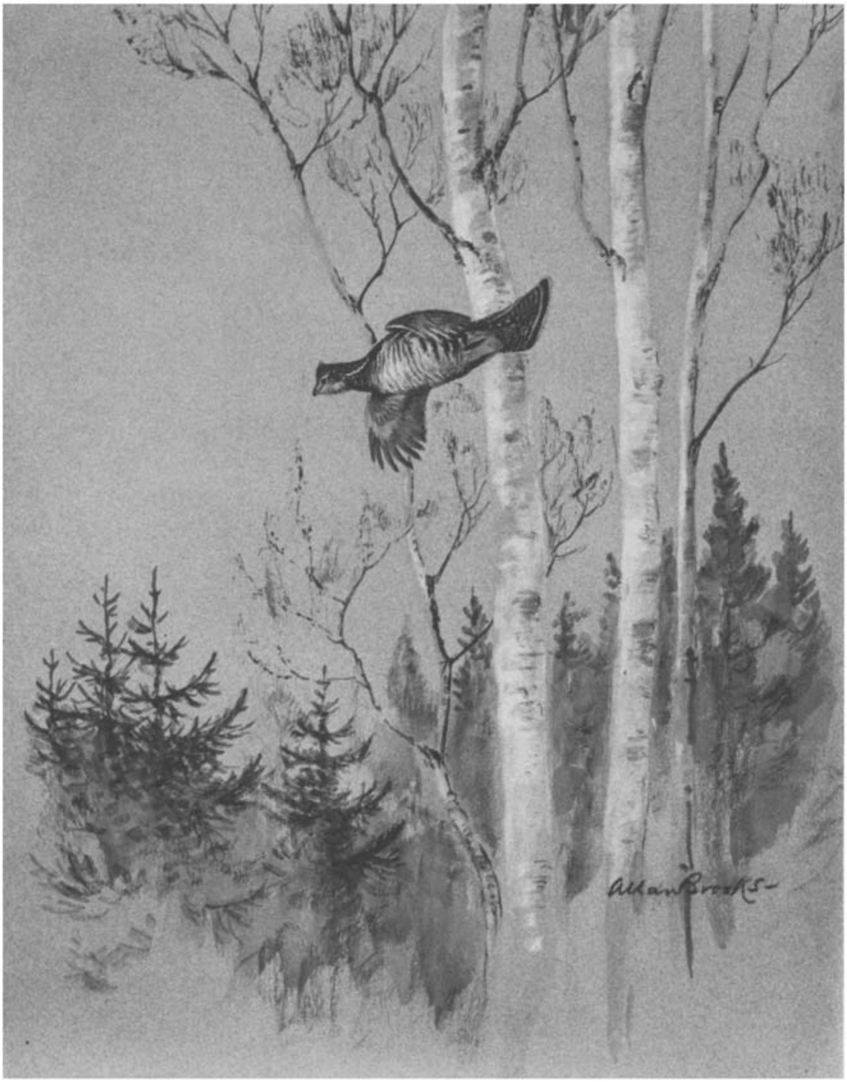
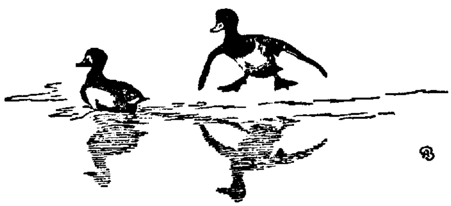

Allan Brooks

GAME MANAGEMENT

Aldo Leopold

With a New Foreword by
Laurence R. Jahn



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TO MY FATHER

CARL LEOPOLD

PIONEER IN SPORTSMANSHIP

"How oft against the sunset sky or moon
We watched the moving zig-zag of spread wings
In unforgotten autumns gone too soon,
In unforgotten springs!"

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FOREWORD

Some who now strive to advance conservation programs are prone to forget that there was a time when there was no field of conservation endeavor. Wild things were something to be overcome and forgotten, not something to be cherished, respected, and managed purposefully to ensure their perpetuation and associated values.

In the United States until about 1905, the prevalent notion of "conservation" was to enact laws to restrict hunting and thereby string out the remnant wildlife supplies and make them last longer. Wildlife was considered as something that must eventually disappear, not as a resource that could be produced at will through prescribed management.

Among the embryonic conservation ideas, concepts, theories, and beliefs of the early 1900s were some that gained broader recognition as the 20th century passed the halfway mark. They included:

- Conservation through wise use, advanced by Theodore Roosevelt and Gifford Pinchot in 1910. Under this doctrine, wildlife, forests, rangelands, and other similar resources were conceived to be renewable, and therefore could be perpetuated if managed on the basis of scientific information. Care of these resources was recognized as a public responsibility, and the ownership of wildlife as a public trust.
- A moral responsibility for perpetuation of threatened forms of wildlife. This was considered among the first major steps in recognizing public values of wildlife.
- Seeking institutional arrangements, means, and measures to maintain and produce wildlife in life communities used by people.

Aldo Leopold's reaction to degraded wildlife and land situations of his time was to produce this monumental book, *Game Management*, first published in 1933. It was fashioned from his belief that through coordination of scientific information and uses of land, wildlife populations could be restored through "creative use of the same tools which have heretofore destroyed it—axe, plow, cow, fire, and gun."

Game Management provides the ideas, principles, techniques, and administrative alignments to encourage land to produce wildlife. It incorporates the philosophies of a sensitive individual with unique perceptions. As Leopold stated in *A Sand County Almanac*, "There are some who can live without wild things, and some who cannot." This book is by a man who could not, one committed to restoring "wild things" and managing wildlife on a sustainable basis.

Findings from the literature were combined with Leopold's personal field experiences to provide in *Game Management* a framework of "factors" and "influences . . . to portray the mechanism which produces all [wildlife] species on all lands, rather than to present the procedures for producing particular species or managing particular lands." These "factors" and "influences" operating on wildlife populations and their environments are as pertinent today as they were when set forth more than five decades ago. They constitute the cornerstone for the science and art of wildlife management. Leopold now is heralded as the "father" of the profession and practice.

That Aldo Leopold visualized more than wildlife/land relationships is clear in his statements: "Every head of wild life still alive in this country is already artificialized, in that its existence is conditioned by economic forces. . . . The hope of the future lies not in curbing the influence of human occupancy—it is already too late for that—but in creating a better understanding of the extent of that influence and a new ethic for its governance. . . . Management is a way to maintain a supply of game, and other wild life, in the face of that [human population] expansion."

Leopold's call, and other calls, for broader recognition of wildlife values have prompted responses and some significant advances in man/wildlife/land relationships. In the 1930s, some people recognized that wildlife could not be perpetuated adequately by laws that only regulated its consumptive use or established refuges for it. Additional legal measures were needed to interject wildlife values into planning a host of land and water developments and uses. With such requirements, alternatives to prevent adverse impacts on wildlife and their habitats could be identified. This approach is precisely what Leopold had visualized must be used to advance wildlife management and what he outlined in *Game Management*.

This strategy and Leopold's principles were encompassed in several federal laws—including the Fish and Wildlife Coordination Act (1934)—designed, in varying degrees, to advance and achieve wildlife conservation. Some statutes, like the Coordination Act, are narrowly drawn and mandate consideration only of impacts on wildlife and fish. Others, like federal pollution laws, seek to maintain the integrity of life communities by maintaining physical, chemical, and biological characteristics required for sustained productivity, including wildlife.

By 1969, the fundamental ideas of Leopold, and those of many others, combined to help lay another profound conservation framework and milestone—the National Environmental Policy Act. Known best by its acronym, NEPA added for the first time precise national requirements for all U.S. federal agencies to consider land/man/wildlife relationships. And it declared several pioneering environmental/conservation policies, including:

- To promote efforts to prevent or eliminate damage to the environment and biosphere;
- To create and maintain conditions under which man and nature can exist in productive harmony;
- To fulfill the responsibilities of each generation as trustee of the environment for succeeding generations;
- To preserve important national aspects of our natural heritage and maintain, wherever possible, an environment that supports diversity; and
- To enhance the quality of renewable resources.

Under NEPA guidelines and regulations, all agencies of the U.S. federal government must utilize a systematic interdisciplinary approach that will ensure the integrated use of natural and social sciences and environmental design arts in planning and decision making that have impact on man's environment. Ecological information, as sought by Leopold, is to be generated and used in evaluating, planning, and implementing federally assisted resource-development projects.

NEPA incorporates an ecological dimension in public administration, building from the ground up, with more careful attention given soils, waters, plants, animals, and people in particular units of the landscape. It brought the environmental impact statement as an action-forcing mechanism to induce an ecological conscience throughout the U.S. federal government's operations. Procedures require an agency to become fully aware of the potential environmental impacts of proposed actions before it approves a development plan. Avoidable adverse environmental impacts are to be foreseen and avoided. Similar policies and requirements also have been enacted in some states and in Canada.

These NEPA policies and processes set in motion a new system in society for integrating wildlife and other similar requirements in ever-intensifying uses of the landscape. Whether Leopold visualized such a comprehensive act and procedural system is unknown. But it is clear that, through *Game Management*, he provided fundamental concepts, philosophies, principles, and insights supportive of the act and embodied in the procedures.

The environmental awareness growth and movement of the 1960s and thereafter provided the growing "public will" to reform attitudes and actions of man toward nature. It spawned society's first broad, major effort (NEPA) to reorient the priorities and responsibilities of government, and to establish a mechanism to prevent adverse impacts to the resource base, including its wild living resources. Public polls in the past two decades show continuing broad concern and strong support for environmental quality and the means and measures to ensure it. Whereas Aldo Leopold had called for integrated resource planning and management, NEPA finally required it. The courts continue to reaffirm the U.S. federal government-wide policy of environmental quality and conservation. Slowly and incrementally, Leopold's land ethic has been and continues to be woven into the fabric of society.

Similar efforts have been made on the international scene. A global environmental ethic has been written into treaties, resolutions, agreements, and administrative practices through the United Nation's system and the good work of the International Union for Conservation of Nature and Natural Resources and others. In all of these advances, the blueprint is for sustainable development and more sensitive resource use.

Wildlife, especially those forms moving among states and countries, must be managed intensively to avoid competition among political entities and excessive exploitation of their populations and supportive habitats. Enactment of the Lacey Act in 1900, the first U.S. federal wildlife statute, reflected the views of conservation program administrators and elected officials that the best way to manage mobile wildlife and fish is through coordinated, cooperative efforts. Leopold propelled the call for such needed efforts, with emphasis on habitat required to produce wildlife.

Early treaties, like those for fur seals (1911) and the first for migratory birds with Great Britain on behalf of Canada (1916), focused on the animals and were silent on the need to maintain the habitats on which the animals depend. A 1936 treaty with Mexico was the first to call for "refuge zones" for migratory birds. The

1974 treaty with Japan focused more closely on habitat by obligating the parties to take measures to maintain and enhance the environment of birds covered by the agreement. The 1976 treaty with the Soviet Union obligated each signatory nation to (1) identify areas of special importance in the conservation of migratory birds, and (2) undertake measures necessary to protect the ecosystems in those special areas against pollution, detrimental alteration, and other environmental degradation. Similar, but not identical, international policies were enacted in the 1970s and 1980s to perpetuate wildlife populations and protect the ecosystems and habitats supporting them. Such conservation provisions now apply from the Arctic (polar bears) to the Antarctic (a variety of wild living resources, including krill, whales, seals, penguins, fish, etc.).

While many federal conservation statutes have been authorized by the U.S. Congress, the Endangered Species Act of 1973 was the first to encompass a truly comprehensive federal wildlife conservation effort, with particular emphasis on habitat protection. It joins *Game Management* (1933) and the NEPA (1969) as significant milestones in the evolution of America's conservation history.

Congressional policy expressed in the 1973 act:

- Encompasses, under the public trust responsibility of government, any member or population of the plant or animal kingdom;
- Recognizes that threatened and endangered species of wildlife and plants "are of aesthetic, ecological, educational, historical, recreational and scientific value to the Nation and people";
- Requires *all* U.S. federal departments and agencies to seek to conserve threatened and endangered species and use their authorities to satisfy the purposes of the act;
- Requires a means whereby the ecosystems on which plants and animals depend may be conserved; and
- Requires that all methods and procedures necessary to restore a threatened or endangered species be used to the extent required to increase their populations and remove the species from formal lists.

While a good number of wildlife populations (deer, elk, pronghorn, Canada goose, trumpeter swan, egrets, herons, etc.) have been restored since the bleak days of the early 1900s using the principles and practices described by Leopold and others, many more await attention, as signaled by those entered on and being added to the formal threatened and endangered species lists. In 1984, for example, 46 new species were added to the U.S. list, bringing the total listed to 828. This includes 331 native and 497 foreign species. More than 2,000 native U.S. species of plants and animals have been identified as candidates for eventual listing. Specific recovery plans have been prepared for 164 species needing restoration.

That habitat is available for wildlife populations to increase is reflected in substantial population gains in the wild turkey and other species. From approximately 130,000 wild turkeys nationwide in 1948, the population expanded to 530,000 in 1968 and to 2 million in the early 1980s, an overall 1,438 percent increase in a third of a century. These gains were registered even as the human population and activities expanded rapidly. Such well-designed and executed wildlife population restoration efforts are successful because approximately 90 percent of the U.S. landscape is not developed excessively, even though most is used for a variety of man's purposes, and wildlife habitat needs mesh with prevailing uses of the landscape. Suitable habitat, combined with strong public support, including citizens reporting poaching incidents and other violations to conservation law enforcement authorities, have provided and can yield future wildlife population increases.

Rather than proceeding with restoration and management of only one species at a time, a second strategy is to focus on units of the landscape (ecosystems) on which groups of threatened and endangered species depend. A similar approach for integrated resource management, as called for by Leopold, has been designed for all wildlife, not just threatened and endangered species. Federal laws, such as the Forest and Rangelands Resources Planning Act (1974), National Forest Management Act (1976), and Federal Land Policy and Management Act (1976), require plans for integrated multiple-use, sustained-yield resource management on federal lands, making up about one-third of the U.S. acreage. Among the standards governing future land management by the U.S. Forest Service are a number of provisions calling for wildlife benefiting considerations and actions. Similar guidelines and requirements for integrated resource management have been or are being developed in individual states, such as Missouri, Minnesota, New York, North Carolina, Oregon, Pennsylvania, and others.

The milestones in conservation, including the cornerstone *Game Management*, have created substantial demands for a wide array of scientific information to use in developing plans for integrated resource management, such as for soil erosion and water pollution control, and farm, ranch, forest, range, and wildlife management. In 1933, Leopold found the concepts and principles sound for moving forward, but the bank of scientific information and management experiences scarce. Fortunately, significant progress has been made in providing essential information.

A substantial number of outstanding publications produced in the half-century after *Game Management* was published now provide insight for foresters and range, wildlife, and other resource managers, including farmers and ranchers, to account for wildlife in land-use planning, in preparing environmental impact statements, and in on-the-ground management. *Guidelines for Increasing Wildlife on Farms and Ranches* (F. Robert Henderson, 1984), as well as publications for maintaining and enhancing wildlife on forests and rangelands in the Blue Mountains of Oregon and Washington (Jack Ward Thomas, 1979), the Rocky Mountain Region (Robert L. Hoover and Dale L. Wills, 1984), and the Great Basin of Oregon (Chris Maser and Jack Ward Thomas, 1985) are milestones. Of equal status are other insightful reports for improving lands for individual species or groups of species, such as *Managing Northern Forests for Wildlife*, especially ruffed grouse, woodcock, deer, and other wildlife (Gordon W. Gullion, 1984). All of these management guidelines respond most effectively to Leopold's call for practical prescriptions to integrate wildlife habitat needs into forest, range, farm, and other land uses. In the past decade (1975–1986), a few states—such as Missouri and Kansas—and Canadian provinces have developed specialized services for managing wildlife in urban/suburban areas.

The volume of sound information on which to base management of wildlife and other natural resources continues to grow. Research on wildlife, barely initiated in the early 1930s, now is recognized—as called for by Leopold—as the fountain for new information to improve reproduction, survival, and management of wildlife. While the legal bases for maintaining wildlife and their life communities are firmer now than in 1933, wildlife remains threatened by habitat degradation and environmental pollution. Impacts of acid precipitation and other hazardous chemical compounds remain to be identified more clearly. Understanding must come to parallel insights developed on the devastating impact of DDT on birds at the upper ends of food chains, such as the peregrine falcon, that led to banning DDT from general use.

Federal and state laws pertaining to pollution of the atmosphere, inland waters, and the high seas, together with regulation of hazardous and toxic wastes, provide at least some measure of consideration for wildlife. Threats to wildlife from such sources are apparent, but it remains to be seen how legal authorities can be translated into affirmative actions benefiting wildlife.

Just as Leopold was limited by the existing knowledge base when preparing *Game Management*, so are resource planners and managers somewhat limited today in information required to advance resource management. Those knowledge limitations emphasize the need for a continuing stream of research to improve the scientific information needed to play an increasing role in public policy and administration.

Two fairly recent developments in techniques have evolved to provide wildlife and other resource managers with better information in formats most useful for making management decisions. The automatic radio-tracking system, developed in the 1950s and 1960s at the University of Minnesota's Cedar Creek Natural History Area, and improved over time, provides critical information on an animal's movements and its behavioral and physiological reactions to ecological conditions.

Electronic data processing capabilities permit rapid analyses of telemetry-generated data and other large volumes of numerical data to produce simulation models. Use of computer-generated simple models, for example those in New York (Aaron N. Moen, 1973), advanced understanding of energy metabolism in white-tailed deer. This fundamental work helped flesh-out Leopold's concepts on seasonal limiting factors and provides a quantitative framework for better understanding characteristics and changes of deer populations, including deer/land/man relationships.

One of the most progressive uses of simulation models has been to assist biologists and resource managers in designing and evaluating hunting regulations and their potential impacts on wildlife populations. Prior to the era of computers, biologists and managers had to complete evaluation of the effects of specific hunting regulations *after* the season to identify whether those regulations achieved desired objectives. Simulation models now can provide the planner, biologist, resource manager, and administrator with an early view of likely results from proposed decisions and associated implementing actions. Realistic and verified simulation models hold much promise for improving management proposals and effectiveness, as well as citizen understanding of management goals and practices.

The development of these and other techniques provide many opportunities to place planning, decision making, and resource management on a firmer factual foundation. Such models, used in combination with adequate environmental assessments or impact statements can spare taxpayers the cost of unforeseen consequences and/or costly restoration.

Leopold's foresight, philosophy, and sensitivity to uses of statistical information serve as a reminder to keep simulation models and their many uses and values in perspective. The biological mechanism of wildlife population increase ". . . is one of those 'scientific subjects' which cannot be concisely described except by means of tables and graphs, but the lay reader should not allow his unfamiliarity with these seemingly dry forms of expression to becloud his realization of the music inherent in their columns and curves. These are, in fact, the code symbols wherewith we may reconstruct the score of a great symphony. Education may be considered a success, and conservation an assured fact, when both layman and scientist can shift their attention from the symbol to the music—can hear with John Muir 'every cell in a swirl of enjoyment, humming like a hive, singing the old new song of creation.'"

Since 1933, the United States and other countries have come to the recognition, sought by Aldo Leopold, of wild animals and plants as essential components of landscape ecosystems. But despite this broad recognition, two examples illustrate pressing needs, among many, for realigning maladjustments of man/wildlife/land relationships through management to ensure wildlife's well-being.

In Alaska, with its vast expanse of wild, spectacularly beautiful landscape, formerly thriving goose populations have been declincing drastically. Left are millions of acres of attractive habitats underutilized or unoccupied by breeding pairs. In the Yukon-Kuskokwim Delta, likely the greatest wild goose breeding area in the world, four goose populations (black brant, cackling Canada goose, white-fronted goose and Emperor goose) have declined from about 1 million in the 1950s to less than half that number in the 1980s. The cackling Canada goose population declined 93 percent from nearly 400,000 in the mid-1960s to less than 30,000 in 1983. Obviously, more effective management is needed to reduce mortality of geese throughout their ranges, restore their formerly abundant populations, and permit nesting geese to make optimum use of available habitats.

Use of geese for food by native people in Arctic and Subarctic nesting grounds reminds resource managers that differing cultures and uses (food, recreational, etc.) of this migratory bird resource must be incorporated in management plans, if the plans are to be most effective. Spring taking of breeding geese and their eggs must be recognized fully, as stated in the James Bay and Western Canadian Arctic agreements, and called for in the North American Waterfowl Management Plan. New patterns of international cooperation and effective management are needed immediately to assure that skeins of geese will continue to proclaim the seasons on their migrations between far northern breeding grounds and southern wintering areas.

In Chesapeake Bay, one of the two outstanding estuaries in the world, man's current activities in the watersheds feeding waters to the 4,400-square mile Bay are incompatible with maintaining the former high biological productivity. Excess nutrients, loss of submerged aquatic vegetation, and pressure of hazardous and toxic compounds now limit production of plants and animals. Commendable cooperative efforts among elected state representatives, resources personnel, local groups of citizens and others are striving to forge new institutional arrangements and management approaches to restore productivity of the famous estuary. Included are actions to have water discharges to the Bay meet quality standards, and to redesign land developments and uses—particularly farming practices—to encourage rehabilitation of the Bay.

Accomplishments in restoring the Bay and the geese, as well as other renewable resources, would make environmental and economic good sense. Success in such cases would demonstrate that appropriate man/land/wildlife relationships can be achieved, as sought by Leopold in his writings.

The stirrings to seek broad realignment of man/land/wildlife relationships initiated in the 1930s and now receiving focused attention in Alaska, the Chesapeake Bay, and elsewhere, were blended into a new national agricultural program through the Food Security Act of 1985. For the first time, a strong conservation dimension was integrated into food and fiber commodity farm programs to correct abusive, disgraceful soil erosion, water quality, and wildlife habitat situations, and place agricultural land use on a more sustainable basis. Unlike other federal agricultural/conservation efforts of the past 50 years, which have poured billions of dollars into marginally effective approaches, the 1985 act uses a new approach. Federal government agricultural program taxpayer-funded subsidies will no longer be available to landowners and operators who allow erosion to continue beyond established standards and limits on their farms.

Management procedures and practices are designed to reduce soil erosion by 50 percent in a few years and assist farmers realign their operations to make them economically and environmentally sound by:

- Removing up to 45 million acres of highly erodible lands from intensive cultivation through the "conservation reserve";
- Preventing vegetated rangelands from being converted to cultivation through the "sodbuster";
- Maintaining wetlands through the "swampbuster";
- Withdrawing commodity (feed grain, wheat, rice, and upland cotton) acreages from production through multiyear acreage set-asides; and
- Providing conservation easements for 50 or more years to cancel part of a farmer's debt where his land is security for a Farmers Home Administration loan.

Lands involved in these reform programs occur as tracts in farms, ranches, and fields in every region of the United States. With restoration and/or maintenance of suitable vegetative cover, many landowner, wildlife, and public benefits should result. Such benefits were sought by Leopold in *Game Management* and through his land ethic. This ethic does not deny the use of resources, but rather advocates the perpetuation of their replenishment through sensitive management.

Although response capabilities to carry out conservation programs have grown in the 50 years since *Game Management* was first released, the growing human population, public expectations, and legal responsibilities have expanded needs for more-intensive resource management. At this present time of economic concern, it is urgent that citizens and their elected and appointed representatives place stewardship and management of the resource base, together with funding and general support for it, on an equal basis with national defense. Sustained uses of the resource base, as perceived by Leopold and others, are required to provide a reasonable standard of living for people and for ensuring capabilities for national defense.

This call for realigning national investments of taxpayers funds parallels those calls made by Leopold and others in the 1930s to improve consideration and management of wildlife and other natural resources. His calls and accumulated responses over a half-century include:

- Training at higher institutions of learning to prepare individuals to be biologists and wildlife managers capable of responding effectively to many types of informational and public service demands. Only a few courses on wildlife management were available prior to 1933. By 1984, there were wildlife curricula in 95 colleges and universities in North America, with enrollment of more than 7,500 students.
- Forming a professional organization to advance competency of practioners and advance the art and science of wildlife management. From the formation of The Wildlife Society in 1937, the organization now numbers more than 8,000 members. In the mid-1980s, there were at least 10,000 and possibly up to 15,000 wildlife professionals with a minimum of a Bachelor's degree in wildlife science.
- Improving research to enlarge the volume of scientific information available to improve wildlife management. From the first Cooperative Wildlife Research Unit established in Iowa with private funds more than 50 years ago, the Unit system has enlarged to more than 20 located on university campuses throughout the United States. In addition, private, state, and other public research centers contribute information for management purposes. This combined effort results in titles of 2,000–2,500 new wildlife publications being entered annually in the computerized U.S. Fish and Wildlife Reference Service system.
- Strengthening organizations and administration of government agencies with responsibilities for wildlife populations and their habitats. From a beginning largely dealing with protection of remnant wildlife through limited conservation law enforcement prior to 1900, government agencies were given additional responsibilities for wild living resources. From single-purpose agencies there emerged agencies with multiple functions. Increasing public demands for wildlife and associated recreational and subsistence uses, prompted establishment of diversified and enlarged well-trained staffs to meet management challenges. Today, every state, territory, and Canadian province has a wildlife agency and

> other resource agencies staffed with well-qualified professionals. All are focusing to varying degrees on ways to integrate wildlife reproduction and survival needs into land and water uses to benefit wildlife populations, their habitats and the public. Citizen concern over environmental quality in the 1960s and 1970s brought substantial changes in wildlife and other government organizations and programs. All wildlife, game and nongame alike, is receiving increasing attention as demands on all resources increase. State and federal responses to meet the challenges of broadening responsibilities have varied, with the process of change continuing to be more responsive to intensive, coordinated, and integrated resource management.

These responses, as well as others, provide some pieces to develop the picture within the overall framework provided by Aldo Leopold in 1933 for integrated wildlife/land/man management. Additional pieces remain to be added, and some of those present need to be modified, as efforts continue to strengthen and refine conservation and management efforts. Continuing positive efforts would respond to Leopold's view that "Conservation is nothing more or less than a purposeful effort to perpetuate and extend . . . [wildlife populations and recreational opportunities among] our standards of living."

Game Management in 1933 identified the fundamental approach, facts, skills, and opportunities for restoring and managing wildlife populations and the natural ecosystems and habitats supporting them. It provided the framework to generate biological/ecological facts needed to provide resource managers and landowners with information required to carry out wildlife/land/man management more effectively. That framework is as pertinent now as some 50 years ago. It provides the outline to factor problems, seek critical information, and reach logical insights, conclusions, and decisions to manage wildlife populations and the habitats and ecosystems that support them. This insightful framework encouraged thoughtful individuals to enlarge field observations to quantitative field studies.

Game Management is a unique book. Not only was it the first—the cornerstone—text on the subject, it still is the only one that provides insight on the history of ideas, philosophies, and procedures used to frame the science and art of wildlife ecology and management. Understanding those historical roots in the search to improve wildlife/land/man relationships is a *must* for any student, biologist, resource manager, or other interested individual.

Aldo Leopold's insights and expressions of ethical and aesthetic values found in wild things are in no other similar text. As he wrote, "By learning how some small part of the biota ticks, we can guess how the whole mechanism ticks. The ability to perceive these deeper meanings, and to appraise them critically, is the woodcraft of the future." He believed firmly that people must learn more about the entire biotic landscape. His conviction for the importance of reading the landscape was exemplified in his personal involvements, including his classroom. There he asked for one's field observations and their meanings. He wanted to stimulate an individual's interest in "reading sign," a rare skill he considered too often seemingly inverse to book learning, and to test a student's comprehension of how the land functions and the biota ticks. These brief "mental whetstone" sessions honed the insights and perceptions of the participants. That same philosophy is continued in *Game Management*, a rare volume indeed.

This unique book continues to serve as a base to stimulate ideas in the crusade for more sensitive, integrated resource management, as called for by Leopold and now a declared international and national mission. In combination with more recent information, it can be used to help develop plans to meet projected increasing U.S. public demands for all forms of wildlife-oriented uses to the year 2030. These citizen desires emphasize that wildlife now is recognized as an important national treasure, as Aldo Leopold believed, requiring and deserving improved intensive management.

VIENNA, VIRGINIA — LAURENCE R. JAHN
March 1986

PREFACE

We of the industrial age boast of our control over nature. Plant or animal, star or atom, wind or river—there is no force in earth or sky which we will not shortly harness to build "the good life" for ourselves.

But what is the good life? Is all this glut of power to be used for only bread-and-butter ends? Man cannot live by bread, or Fords, alone. Are we too poor in purse or spirit to apply some of it to keep the land pleasant to see, and good to live in?

Every countryside proclaims the fact that we have, today, less control in the field of conservation than in any other contact with surrounding nature. We patrol the air and the ether, but we do not keep filth out of our creeks and rivers. We stand guard over works of art, but species representing the work of æons are stolen from under our noses. We stamp out the diseases of crops and livestock, but we do not know what ails the grouse, or the ducks, or the antelope. In a certain sense we are learning more rapidly about the fires that burn in the spiral nebulæ than those that burn in our forests. We aspire to build a mechanical cow before we know how to build a fishway, or control a flood, or handle a woodlot so it will produce a covey of grouse.

Control comes from the co-ordination of science and use.

This book attempts to explore the possibilities of such co-ordination in a single, limited field—the conservation of game by management. Its detail applies to game alone, but the principles are of general import to all fields of conservation.

The central thesis of game management is this: game can be restored by the *creative use* of the same tools which have heretofore destroyed it—axe, plow, cow, fire, and gun. A favorable alignment of these forces sometimes came about in pioneer days by accident. The result was a temporary wealth of game far greater than the red man ever saw. Management is their purposeful and continuing alignment.

The conservation movement has sought to restore wild life by the control of guns alone, with little visible success. Management seeks the same end, but by more versatile means. We seem to have two choices: try it, or hunt rabbits.

Game management has long been an empirical art in Europe, but the attempt to adapt that art to biological principles and to American conditions and traditions, is new. Facts about game have been accumulating for a long time, but there has been only one previous attempt to synthesize from those facts a coherent system of principles. Adams, in his *Importance of Wild Life in Forestry*, presents exhaustive statistics on the economic value of wild life, and interprets them in terms of biological principles, but he does not deal with the technique of altering range for greater productivity, which is the principal subject of this volume.

Few biological arts depend as much on ingenuity and resourcefulness as this one. It is still in the stage where each practitioner must create his own skill rather than absorb that of others. This will always be true of the element of woodcraft, which can never be included in any book.

Few of the techniques described in this volume have been tested sufficiently in practice to be safely followed verbatim. They represent examples of how to think, observe, deduce, and experiment, rather than specifications for what to do. Incomplete or tentative information is freely included, but with due care to differentiate those many degrees of certainty which lie between opinion and established fact. It is hoped that this emphasis on the paucity of existing knowledge of game will stimulate efforts to increase it.

To encourage the reader to interpret for himself the evidence bearing on management questions, a rather full bibliography, and frequent references to it, have been included. The starred items are recommended as general reading.

The subject matter of this volume has been hung upon a framework of "factors," rather than of species or land units, because the object is to portray the mechanism which produces *all* species on *all* lands, rather than to prescribe the procedures for producing particular species or managing particular lands. The former function belongs to the species monograph, of which we already have an outstanding example in Stoddard's *Bobwhite Quail.* The latter is the function of the local manual or handbook, such as the *Management of Upland Game Birds in Iowa.*

The particular set of "factors" and "influences" here set down as determining abundance is of course only one of many possible ways of depicting the biological forces which the art seeks to control. Many years of thought, however, have proved these categories consistent and convenient. They were first conceived by the author as a personal hobby while in the employ of the United States Forest Service in Arizona and New Mexico. A manuscript on *Game Management in the Southwest* was prepared in 1925, but never published.

The needed opportunity to test the same set of ideas in a new region, and clothe them with more detail, occurred when the author was employed from 1928 to 1931 by the Sporting Arms and Ammunition Manufacturers' Institute to make a game survey. The *Report on a Game Survey of the North Central States* is built upon the definitions and principles outlined herein, also the later *Game Survey of Iowa.*

In 1929 the same ideas were presented in a series of lectures at the University of Wisconsin.

Part of Chapter I appeared in *Outdoor America* for June, 1931; part of Chapter III in *The Canadian Field-Naturalist* for October, 1931; part of Chapter V in *The Journal of Forestry* for October, 1931; part of Chapter XVI in *American Game* for March-April, 1931.

This volume aspires to a three-fold function:

First, to serve as a text for those practicing game management or studying it as a profession.

Second, to interpret for the thinking sportsman or nature-lover the significance of some of the things he sees while afield with gun or glass, or does in his capacity as a voting conservationist.

Third, to explain to the naturalist, biologist, agricultural expert, and forester how his own science relates to game management, and how his practices condition its application to the land.

In short, this is an attempt to describe the art of cropping land for game and to point the way toward its integration with other ends in land-use.

ALDO LEOPOLD.

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PART I

MANAGEMENT THEORY

Chapter I

A HISTORY OF IDEAS IN GAME MANAGEMENT

Game management is the art of making land produce sustained annual crops of wild game for recreational use.

Its nature is best understood by comparing it with the other land-cropping arts, and by viewing its present ideas and practices against a background of their own history. This chapter compares game management with other forms of agriculture, and sketches its evolution in space and time.

Comparisons. Like the other agricultural arts, game management produces a crop by controlling the environmental factors which hold down the natural increase, or productivity, of the seed stock.

The various arts differ greatly, however, in the degree of control which they attempt to exert, and in the nature of the seed stocks which they grow.

Game management and forestry employ natural species. The bobwhite quail produced by management, and the mature white pine produced by silviculture, are indistinguishable in both form and behavior from their aboriginal progenitors. Compare these now with the products of horticulture, agronomy, and animal husbandry. Who would recognize, without being told, the identity in origin of the Yellow Dent corn and the lowly teosinthe; of a Hereford steer and a wild ox; of a Grimes Golden and the wild apple of Eden?

Game management and forestry grow natural species in an environment not greatly altered for the purpose in hand, relying on partial control of a few factors to enhance the yield above what unguided nature would produce. Their controls are barely visible; an observer, unless he were an expert, could see no difference between managed and unmanaged terrain. Hence their success depends more on the exercise of skill in the selection of the right factors and the right controls, than on heavy investments of labor or materials.

The other forms of agriculture, on the other hand, more or less completely rebuild the environment by cultivation, so that the crop competes with nothing but itself, and must usually be replanted each year. Most domesticated plants and animals are incapable of survival in the wild state, much less of perpetuating themselves as wild populations.

Game farming is an intensified form of game management which propagates wild species in confinement, usually for later release as wild seed stock, or as a supplement to the wild crop.

In game, as in forestry and agriculture, there is no sharp line between the practice which merely exploits a natural supply, and the practice which harvests a crop produced by management. Any practice may be considered as entitled to be called game management if it controls one or more factors with a view to maintaining or enhancing the yield.

The definition of game management which opens this chapter specifies *wild* game *for recreational use*. The purpose of attaching these specifications is to introduce, at the outset, a qualitative as well as a quantitative criterion of what constitutes successful practice. The production of tame game for use as meat is animal husbandry. Its harvesting is hardly recreation. A later chapter on esthetics asserts that the recreational value of game is inverse to the artificiality of its origin, and hence in a broad way to the degree of control exercised in its production.

There are all degrees of control. What degree represents the best compromise between quantity and quality is a perplexing problem in esthetics and social engineering. It seems reasonable to accept some moderate degree of control, rather than to lose species, or to suffer the restriction of sport to those financially able to follow the wholly wild game of the shrinking frontier into other lands. A discussion of these questions will follow in Chapter XVI.

History shows that game management nearly always has its beginnings in the control of the hunting factor. Other controls are added later. The sequence seems to be about as follows:

1. Restriction of hunting.
2. Predator control.
3. Reservation of game lands (as parks, forests, refuges, etc.).
4. Artificial replenishment (restocking and game farming).

5. Environmental controls (control of food, cover, special factors, and disease).

North America has reached the stage where controls of the fifth class are becoming necessary. The present game conservation movement is groping toward the realization of this fact.

Evolution in Europe and Asia. The practice of some degree of game management dates back to the beginnings of human history. Taverner (1930) has pointed out that laws for the regulation of hunting have their origin in the tribal taboos which grew up in the early stages of social evolution. The tribes observing taboos which were biologically effective in preserving the game supply were more likely to survive and prosper, he believes, than the tribes which did not. In short, hunting customs, like plant and animal species, were evolved by a process of selection, in which survival was determined by successful competition. Game laws grew out of these hunting customs.

The first written restriction on the taking of game is probably that contained in the Mosaic Law. In the Book of the Covenant, in which are detailed "the statutes and the judgments which ye shall observe . . . in the land which the Lord . . . hath given thee to possess," Moses decrees:

> "If a bird's nest chance to be before thee in the way, in any tree or on the ground, with young ones or eggs, and the dam sitting upon the young, or upon the eggs, thou shalt not take the dam with the young: thou shalt in any wise let the dam go, but the young thou mayest take unto thyself; that it may be well with thee, and that thou mayest prolong thy days." (Deuteronomy 22 : 6.)

The plainly implied intent is conservation of the "dam" or hen as breeding stock. The phraseology is as circumstantial and repetitive as the act of any modern legislature, save only for the discreet omission of what shall be done with eggs. However, even modern "Committees on Fish and Game" have been known to be ambiguous.

The Mosaic game law was evidently an advance beyond that of his Egyptian taskmasters, whose spirited depiction of hunting scenes shows them to have been keen sportsmen (Pratt, 1923), but whose records reveal no worries over the conservation of sport.

The Greeks and Romans had game laws, but the objective was not the conservation of sport. Solon forbade the Athenians to hunt, because they "gave themselves up to the chase, to the neglect of the mechanical arts." Not all of the Greek leaders, however, were so strait-laced. Xenophon, in an oft-quoted passage, asserts:

> "Men who love sport will reap therefrom no small advantage . . . it is an excellent training for war. . . . Such men, if required to make a trying march . . . will not break down; . . . they will be able to sleep on a hard bed and keep good watch over the post entrusted to them. In advance against the enemy they will . . . obey their orders, for it is thus wild animals are taken. . . . They will have learned steadfastness; . . . they will be able to save themselves . . . in marshy, precipitous, or otherwise dangerous ground, for from experience they will be quite at home in it. Men like these . . . have rallied and fought against the victorious enemy . . . and have beaten them by their courage and endurance."

Thus, as between Solon and Xenophon, we have the first emergence of that still mooted question: Is sport an asset to society?

The Roman emperor Justinian recognized the right of an owner of land to forbid another from killing game on his property, but the issue was one of trespass, not conservation. We find no game management in the Græco-Roman culture.

Curiously enough the first clear record of a well-rounded system of game management for conservation purposes is found not in Europe, but in the Mongol Empire. Marco Polo, in the narrative of his travels across Asia, thus describes the game laws of Kublai, "The Great Khan" (A.D. 1259–1294):

> "There is an order which prohibits every person throughout all the countries subject to the Great Khan, from daring to kill hares, roebucks, fallow deer, stags, or other animals of that kind, or any large birds, between the months of March and October. This is that they may increase and multiply; and as the breach of this order is attended with punishment, game of every description increases prodigiously."

The phrase, "this is that they may increase and multiply," leaves no doubt as to the intent of Kublai's edicts.

Kublai's technique had already evolved beyond mere control of hunting. Near the city of Changanoor in Cathay, Marco Polo found on the Khan's preserves great food patches and a complete system of winter feeding and cover control. He relates that:

"At this place . . . there is also a fine plain, where is found in great numbers, cranes, pheasants, partridges, and other birds. He [the Khan] derives the highest degree of amusement from sporting with gerfalcons and hawks, the game being here in vast abundance.

"Near to this city is a valley frequented by great numbers of partridges and quails, for whose food the Great Khan causes millet, and other grains suitable to such birds, to be sown along the sides of it every season, and gives strict command that no person shall dare to reap the seed; in order that the birds may not be in want of nourishment. Many keepers, likewise, are stationed there for the preservation of the game, that it may not be taken or destroyed, as well as for the purpose of throwing the millet to the birds during the winter. So accustomed are they to this feeding, that upon the grain being scattered and the man's whistling, they immediately assemble from every quarter. The Great Khan also directs that a number of small buildings be prepared for their shelter during the night; and, in consequence of these attentions, he always finds abundant sport when he visits this country; and even in the winter, at which season, on account of the severity of the cold, he does not reside there, he has camel-loads of the birds sent to him, wherever his court may happen to be at the time."

This is the earliest known instance of food and cover control combined with restrictions on hunting. Its completeness implies a long previous course of evolution. Although now six centuries old, it sets a pace in management technique which our most modern state would be hard pressed to follow. Kublai's ideas of democracy in sport are of course another matter. They would need some revision.

Game management in feudal Europe, a century after the days of Kublai Khan's food patches, had not yet learned to control either food or cover. It had, however, developed the regulation of hunting (in the interests of the ruling class) to a high degree—so high that the rebellion of the "one gallus" yeomanry, as personified by Robin Hood, ultimately constituted one of the forces which overthrew the feudal system. These hunting controls began as customs rather than laws. A minute and circumstantial account of such customs is given by Edward, second Duke of York, Master of Game to his cousin, Henry IV, in his *litel symple book*, *Master of Game*, written between 1406 and 1413. (Incidentally this same Edward appears as villain in Shakespeare's *Richard II*. He met his death as a leader of the English vanguard at Agincourt in 1415.)

Edward clearly shows that custom, not law, more or less definitely delimited open and closed seasons for big game. Thus the hart or red-deer season opened at St. John's tide (June 24) and ended on Holyrood Day (September 14). This was the period when the hart was "in grease," *i. e.*, was fattest and best fit for meat. The season evidently ended with the rut, when the meat became strong. The idea of conservation was apparently absent or subordinate.

Written laws establishing closed seasons for conservation purposes go back, in England, at least to Henry VIII, who decreed protection for waterfowl and their eggs from May 31 to August 31. James I added pheasants and partridges. Non-game birds were apparently not protected until 1831.

Hunting custom in Edward's time decreed something equivalent to the modern buck law. A "warrantable hart" was defined as a "hart of ten" (points). Lesser stags (staggards), yearlings (bullocks), fawns (calves), and does (hinds), were either not killed at all, or only during the great drives in which the King participated. All of these lesser sex and age classes collectively constituted "rascal," or unwarrantable deer.

A distinction was drawn between "dry" and "wet" hinds—the former being warrantable, but only during the *winter* (September 14 until Lent), rather than during the hart season of summer and fall.

Hunting custom definitely limited permissible methods and equipments. Edward points out that "beyond the sea" (France) deer were taken

> "with hounds, with grey hounds, and with nets and with cords, and with other harness, with pits and with shot (bows) and with other gins (traps). . . . *But in England they are not slain except with hounds or with shot.*"

It is not clear whether the English taboo on "other gins" was a game conservation measure or a class distinction. Which-ever it was, there rings in Edward's "But in England" that same clear note of the sportsman's disdain for improper methods which still adorns many a hunting tale.

By the time of Henry VII the limitation of equipments had gained definite legal form. Herons could not be taken except by hawk or long bow. Limitation of hours began with Elizabeth's prohibition of night hunting of pheasants. The gradual restriction of equipments and abusive practices progressed in England to the prohibition of pole-traps in 1904, and of bird lime in 1925.

Did management in feudal England control any factor other than hunting? Edward leaves us in doubt. He says that wolves, foxes, wildcats, etc., were hunted as vermin, but there is no clear statement whether vermin-control was for game management purposes, or merely for sport, or for the protection of livestock. Otters, it is clear, were hunted for the protection of fish. Edward points out that:

> "No fish can escape them. . . . They do great harm, especially in ponds and in stanks, for a couple of otters . . . shall well destroy the fish of a great pond or great stank, and *therefore men hunt them.*"

Public bounties as a means of controlling predators came into use much later. *Game and Gun* (February, 1931) points out that Henry VIII placed a bounty on crows, choughs, and rooks. He assessed the bill against the local landowners. Elizabeth, however, empowered church wardens to levy a tax on land, and with the funds thus procured to pay public bounties not only on these birds, but also on pie, stare, martyn hawk, fursekyte, moldkyte, buzzard, shag, cormorant, ringtail, irin, rave, kingfisher, bullfinch, fitchew, polecat, weasel, stoat, wildcat, or other "ravening birds and vermin." Evidently fishermen and orchardists had caught the contagious idea that vermin were responsible for their short crops. Thus do proscription lists tend to grow during the pre-biological stages of management. Later, with the advent of biological research, they invariably tend to shrink.

To revert to Edward and the fifteenth century: Were there any controls of cover and food in those days? Apparently not. Numerous hunting parks or forests, though, had long since been established. The idea of setting aside areas for the benefit of privileged hunters goes back into the remote past, and apparently grew by slow degrees into the idea of setting aside areas for the benefit of the game, and finally into the idea of protecting all landowners against trespass, so that each would have an incentive to manage his own game. Trespass penalties of almost savage severity mark the beginning of the process. Penalties only heavy enough to sustain the landowner's incentive mark its later stages. *Public* reservations for conservation purposes appear at a very late stage.

English hunting reservations for the privileged, as described by Malcolm and Maxwell (1910) and Johnson (1819) were first formally recognized in a "charter of the forest" granted by Canute the Dane in 1062. William the Conqueror and his successors "did daily increase those oppressions by making more new forests in the lands of their subjects, to their great impoverishment" until "the greatest part of the kingdom was then converted into forests."

These hunting reservations were of two kinds.

A "forest" was the exclusive prerogative of royalty, and was governed by special forest laws. A forest consisted of:

> "A circuit of woody grounds and pastures, known in its bounds as privileged for the peaceable being and abiding of wild beasts and fowls of forest, chase, and warren, to be under the king's protection for his princely delight, bounded with irremovable marks and meres . . . replenished with beasts of venery and chase, and great coverts of vert for succour of said beasts; for preservation thereof there are particular laws, privileges, and officers belonging there unto."

A "chase" was a similar tract but might be held by a subject, and was protected only by the common law.

As early as 1229 the number of royal "forests" began to be curtailed, while by 1617 most of them had dissolved.

Henry VII (1485–1509) was the first English king to recognize that the common landowner might wisely be granted protection from trespass. He forbade the taking of pheasants and partridges on other people's land without the permission of the owner. James I (1603–1625) extended this to all shooting on all land. Here was the first "owner's permission" trespass law.

The Roman emperor, Justinian, had recognized the same legal principle centuries before, but with him it was a matter of landowner's rights, not a matter of incentive for game production. These English enactments, however, clearly imply that the welfare of game was one of their objectives.

When our modern state legislators in solemn conclave debate whether such "owner's permission" trespass laws are necessary, do they realize that they are coping with no new question, but rather one which came up in Roman times, and was settled in England three centuries ago?

James I apparently first applied the reservation idea for the benefit of the game, as distinguished from that of the hunter. An act passed in his reign decreed that "hail shot in hand guns" (to wit: a shotgun) might not be discharged within 600 paces of a heronry. Here was, in effect, a publicly established breeding refuge.

Henry VIII had long before, in 1536, closed an area near his Westminster Palace, in what is now metropolitan London, to shooting of pheasants, herons, and partridges. Whether this was just a little shooting preserve for his own use, or whether it was a real refuge, is not disclosed. The same doubt pertains to many a minor "refuge" today.

The first breeding refuge for non-game birds was decreed by Parliament in 1869.

Artificial rearing of game for restocking coverts may have begun as early as 1523, when the account book for Henry VIII's privy purse shows that on December 22 he paid a small sum to the "french preste the *fesaunt breeder* for to buy him a goune." It is clear enough that this "french preste" was the keeper of the royal pheasantries, but Maxwell points out that these may have been maintained for aviary or culinary, rather than restocking, purposes. Maxwell says, "It is less than a century since the practice of rearing pheasants became at all well known in this country."

Artificial propagation of mallard ducks, Maxwell points out, dates back to 1631. A letter of that date, accompanying a delivery of 200 eggs, leaves little doubt that propagation was resorted to for purposes of sport (hawking) and on a considerable scale.

We may note in passing that the first mention of artificial propagation coincides in date with the first revival of the Mosaic prohibition of robbing wild nests. Henry VIII set up severe penalties for the possession of wild eggs (Johnson, p. 314). "Bootleg" eggs are still the bane of the English gamekeeper.

Deliberate controls of cover and food in Europe can be assigned no definite date of beginning. Negative controls, *i. e.*, prohibiting destructive practice, began long before positive controls, *i. e.*, the building up of damaged land. Thus William and Mary in about 1694 prohibited the burning of nesting cover in spring (Johnson, p. 294), but I can find no clear instance of systematic cover improvement previous to the beginning of heather control on the Scotch grouse moors, which *The Grouse in Health and Disease* (1911) and Maxwell both say occurred between 1850 and 1873. (The former authority will hereafter be cited as *The Grouse Report.*) Prohibition followed long after by restoration appears to be a fixed sequence of human thought and action on conservation affairs.

Cover control to facilitate shooting is clearly earlier, at least on the continent, than cover control to enlarge the game crop. Malmesbury mentions well-developed "remises" on Hungarian estates in 1799 and 1800, also grain-baiting of wild boars to decoy them within range of blinds. While convenience in shooting was the main idea in these remises, the idea of controlling vegetation to enhance the game crop was evidently not wholly absent. Malmesbury mentions "a small remise *sown* with broom and high grass," in which he and his party killed 96 partridges and 16 hares. Possibly all these remises were to some degree "sown" or "hand made." He describes one as "an English mile long, and about half as wide—covered with high grass, clumped with copse wood, fern, and broom—so that the game lay well." There is possibly an objective inference in the word "clumped." Incidentally he mentions that 1200 head of pheasants, partridges, and hares had been killed in this remise the year before, whereas on the day he hunted it "only" 408 head were killed. The former figure, if his dimensions were right, means an annual yield of four head of small game per acre.

European game management today seeks to control all of the factors determining wild populations. Many American sportsmen have the mistaken impression that European game management relies largely on artificial propagation. Artificial rearing, to be sure, is widely used for pheasants, but in eastern Europe, and probably also elsewhere, wild management or "environmental controls" are used exclusively for all species, including pheasants, with entire success. Maxwell says that even in England a few landowners produce their pheasants entirely by wild management. Artificial propagation is never used for British grouse, and to only a small extent for gray partridge.

Although management in Europe came first and biology afterward, there is plenty of evidence that biological guidance is now increasingly sought as a means of making management more effective, and fairer to non-game species of wild life. The Grouse Report represents the first comprehensive attempt to apply science to the control of the disease factor. While the disease cycle still periodically decimates the British grouse, recovery has been speeded up to such an extent that only a third of the years fall below 50 per cent of normal in yield.

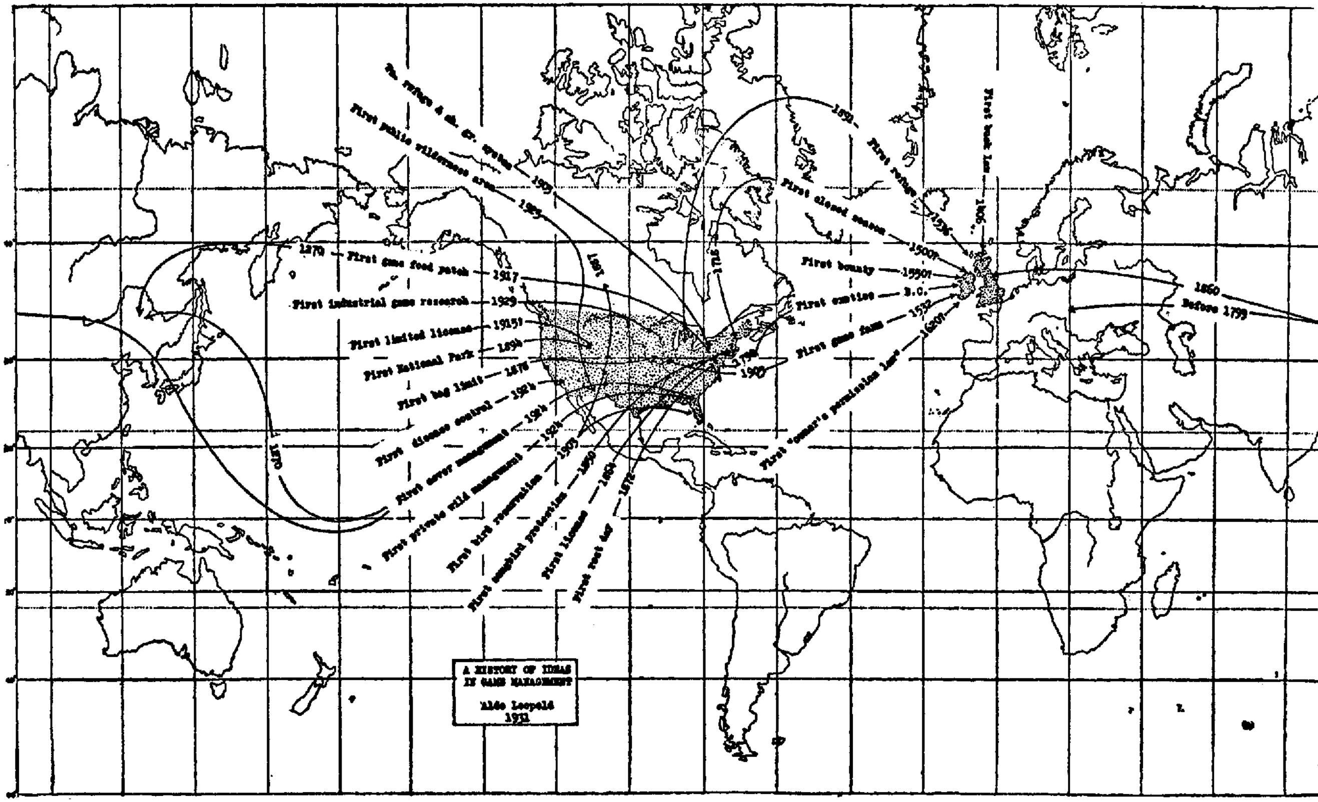
Evolution in America. The history of American management is until recently almost wholly a history of hunting controls. The sequence and direction of their development, from the Revolution up to 1911, is set forth in Palmer's admirable *Chronology and Index* (1912). Palmer points out that at the time of the Revolution, 12 of the 13 colonies had enacted closed seasons on certain species, while several had also prohibited certain destructive equipments and methods, and the export and sale of deerskins. The first closure for a term of years was placed on Massachusetts deer in 1718. The beginning of a warden system appeared in Massachusetts and New Hampshire about 1850. The first protection for non-game birds appeared in Connecticut and New Jersey in 1850.

The enactment of state game laws followed close on the heels of the retreating frontier, reaching the Pacific in California in 1852. By 1880 all of the states had game laws. The first bag limit (25 prairie chickens per day) appeared in Iowa in 1878; the first rest day in Maryland in 1872. Market hunting was first tabooed by Arkansas in 1875.

A hunting license was first required by New York in 1864; a non-resident license by New Jersey in 1864.

Federal supervision of interstate game began with the Lacey Act, which in 1900 prohibited interstate commerce in illegal game. It was followed by our present migratory bird bills, which were introduced in 1904 and 1908, but not passed until 1913. These bills, having been questioned on grounds of constitution-

FIG. I



Outline map, courtesy of Rand McNally.

ality, were finally anchored to the Constitution by the Canadian treaty of 1916.

This partial review of the sequence of American ideas deals, it will be observed, wholly with *restrictions* on when, what, and how one might hunt, and with the organization and financing of enforcement agencies.

We have next to trace the sequence of development in America of the complementary idea of *production* or cropping of game, either by artificial propagation or by environmental controls.

It has no fixed date or point of origin.

The first American plantings of exotics, as traced by Phillips (1928) took place about 1790, when one Richard Bache, a son-in-law of Benjamin Franklin, planted Hungarian partridges on his New Jersey estate. These early plantings were doubtless motivated not so much by a shortage of native game as by a residual affection for the wild life of "the old country," or else by that queer desire to possess something new which all flesh is heir to.

The first state game farm would be a defensible point of origin for the production or cropping idea. This, according to Palmer, was established in Illinois in 1905.

The first refuge would be another logical point. The word "refuge" as a device used in game management did not come into use until about 1910, but the group of ideas now associated with that word was in practice much earlier. The whole modern mechanism of a refuge for ducks, including a strand of wire for a boundary, feed placed inside, and a sunset rule on the surrounding ground, was in effect on Weber's Pond, in the Horicon Marsh, Wisconsin, in 1891. Jack Miner (1923, p. 58) started his now famous waterfowl refuge at Kingsville, Ontario, in 1907, and Allen Green his refuge at Oakville, Iowa, in the same year. Pennsylvania established her first state refuge for upland game in 1905.

The first national park closed to hunting (Yellowstone, 1894) or the first national game reservation (Wichita, 1905) or bird reservation (in Canada, Last Mountain Lake, 1887; in the United States, Pelican Island, 1903) might also be selected as marking the American origin of environmental controls for wild life. Refuges, parks, and reservations, however, may more truly be considered as half-way points between the restrictive idea and the idea of environmental controls. Another half-way idea is that of limiting the kill to the annual increase. The first public attempt to apply this principle, doubtless borrowed either from foresters or stockmen, was Wyoming's issue of "limited licenses" for moose about 1915.

The first public control of food supply by artificial food patches occurred on the Pennsylvania refuges in 1917. By 1920 state food patches were being installed on a considerable scale.

The first public control of a game disease epidemic was the stamping out of hoof-and-mouth disease by the Bureau of Animal Industry after its outbreak in the deer herd of the Stanislaus National Forest of California in 1924.

The first public predator control for game purposes is so thoroughly fused with livestock predator control that no dates can be set. Bounties on predators go back indefinitely. Appropriations for government trapping date from 1915.

The first large-scale private practice of game management, in the sense of a rounded-out system of control of all actionable factors, based on a preceding scientific life-history investigation, was instituted by Herbert L. Stoddard on the South-Georgia Quail Preserves during the period 1924–1928.

The large-scale practice of public game management on publicly owned shooting grounds began on the National Forests at an indeterminate date (since 1910), and in Pennsylvania about 1919.

In short, during the last two or three decades, restrictive legislation has been gradually reinforced by the growth of the idea of production through environmental controls. The production idea is as yet still in its infancy.

This evolution of technique from custom toward law, and from restriction toward production, does not of itself suffice for an understanding of the game movement in America today. Of even greater importance is the evolution of the objectives toward which the technique is applied, and the evolution of scientific tools for its improvement.

The Conservation Idea. European game management for centuries had one simple and precise objective: the improvement of hunting for and by the private landholder.

In America the dominant idea until about 1905 was to *perpetuate*, rather than to improve or create, hunting. The thought was that restriction of hunting could "string out" the remnants of the virgin supply, and make them last a longer time. Hunting was thought of and written about as *something which must eventually disappear*, not as something which might be produced at will.

Our game laws under the restrictive idea were essentially a device for *dividing up* a dwindling treasure which nature, rather than man, had produced. Naturally enough, the policy of division strongly reflected the democratic ideas underlying our political system. Here was something new under the sun: a game system based on an equally distributed citizenship, rather than, as in Europe, on an unequally distributed landownership.

But the passing years made it more and more apparent that this novel system, however admirable in theory, had in practice failed to halt the accelerating decline in game supply. Public-spirited sportsmen groped earnestly for new formulas. The direction of their search was to develop more perfectly the restrictive idea. Better law enforcement and prohibition of market hunting were decided to be the way out.

The game literature of the closing century is saturated with these two ideas. They became personal dogma and public law. "Game protection" became a "Cause." The game hog and the market hunter were duly pilloried in press and banquet hall, and to some extent in field and wood, but the game supply continued to wane.

Came then Theodore Roosevelt, with the idea of "conservation through wise use." Wild life, forests, ranges, and waterpower were conceived by him to be *renewable organic* resources, which might last forever if they were *harvested scientifically, and not faster than they reproduced.*

"Conservation" had until then been a lowly word, sleeping obscurely in the back of the dictionary. The public had never heard it. It carried no particular connotation of woods or waters. Overnight it became the label of a national issue.

The Roosevelt doctrine of conservation determined the subsequent history of American game management in three basic respects:

1. It recognized all these "outdoor" resources as one integral whole.
2. It recognized their "conservation through wise use" as a

public responsibility, and their private ownership as a public trust.
3. It recognized science as a tool for discharging that responsibility.

It left cloudy, however, the question of what kinds of game could best be renewed under public initiative, and what kinds by public encouragement and regulation of private initiative. In big game, Roosevelt correctly forecast a combination of private preserves and public shooting grounds. He wrote in 1909:

"Game preservation may be of two kinds. In one the individual landed proprietor, or a group of such individuals, erect and maintain a private game preserve, the game being their property just as much as domestic animals. Such preserves often fill a useful purpose, and if managed intelligently and with a sense of public spirit and due regard for the interests and feelings of others, may do much good, even in the most democratic community. But wherever the population is sufficiently advanced in intelligence and character, a far preferable and more democratic way of preserving the game is by a system of public preserves, of protected nurseries and breeding grounds, while the laws define the conditions under which all alike may shoot the game and the restrictions under which all alike must enjoy the privilege. It is in this way that the wild creatures of the forest and the mountain can best and most permanently be preserved."

The small-game question was left in uncertain status. Subsequent evolution, however, is gradually answering the whole question. The trend is toward recognizing land-value and mobility as the criteria of public vs. private game management. Migratory birds (mobile, and often occupying cheap lands) became a national charge in 1916. The present moment is seeing the emergence of the idea that forest game (mobile, and on cheap land) can be largely a public charge, whereas farm game (non-mobile, and usually occupying expensive land) can only be managed by private initiative under public regulation (American Game Policy of 1930).

Science as a Tool. Roosevelt's idea of science as a tool for conservation seems a truism to us now, but it was new in 1910. It may be well for the reader to be reminded of the human history interwoven with its growth.

The early naturalists of the two centuries preceding the birth of "Conservation" regarded a species as one of the phenomena of nature which needed to be discovered, catalogued, and described. They realized, and marvelled, that

> "For it the Earth lay preparing quintillions of years
> Without one single animal or plant.
> For it the revolving centuries truly and steadily rolled."

"Gentlemen, look at this wonder," they said, as they held up a new discovery. Then they set about to catalogue it, comfortably assuming that only the same blind forces which had caused it to be there, could, in the fullness of time, cause it to perish from the earth.

But it soon became evident that a species did not continue or discontinue its existence, like a planet or a geological stratum or a sunset, regardless of what the scientist thought or did about it.

This "civilization" which at one moment held it up, saying, "Gentlemen, look at this wonder," might next throw it down and destroy it with all the nonchalance of a glacial epoch.

The naturalist's first response to the realization of this anomaly was to heave a sigh and hasten the completion of his cataloguing, lest by chance some species disappear before receiving the baptism of a Latin name. In some instances, like that of the Arizona elk, this actually happened.

With the Rooseveltian era, however, came the Crusader for conservation, a new kind of naturalist who refused to stomach this anomaly. He insisted that our conquest of nature carried with it a moral responsibility for the perpetuation of the threatened forms of wild life. This avowal was a forward step of inestimable importance. In fact, to any one for whom wild things are something more than a pleasant diversion, it constitutes one of the milestones in moral evolution.

Game management is merely an attempt to deal with the corollary question: How shall we conserve wild life without evicting ourselves?

The Crusaders wrote many volumes, but these told us why rather than how wild life and civilization should be adjusted to each other. These men were mostly biologists, but strangely enough their technique was not biological. It was, rather, an intensification of the pre-existing idea of protective legislation, which experience has now shown does not alone suffice, even when enforced. It retards, but does not reverse, the forces of destruction.

Our sporting literature fell in line with the Crusaders, but pioneered no extensions of their ideas. It consisted for a long time of mildly pleasant hunting yarns, sometimes of literary merit, which hoped with varying degrees of fervency that there would be some game left for our sons, and recommended with varying degrees of skill more laws to retard the day of reckoning. One periodical, *The Game Breeder*, broke away at an early date and pioneered the idea of game production through private initiative, but it leaned toward artificialized game-farming technique, and toward open markets to reinforce the private production incentive. These two corollaries, particularly the latter, beclouded the intrinsic merit of the central idea. This periodical must, however, be credited with the origin of the private initiative idea in America. Its program had the outstanding merit of realism and of constructive discontent with pious phrases.

So far we have the scientist, but not his science, employed as an instrument of game conservation. I do not know who first used science creatively as a tool to produce wild game crops in America. Roosevelt had it in mind as a guide for game regulatory measures, and of course knew of its use for environmental controls in forestry. The idea was doubtless conceived by some one long before it was first successfully applied by the Biological Survey to quail management in Georgia.

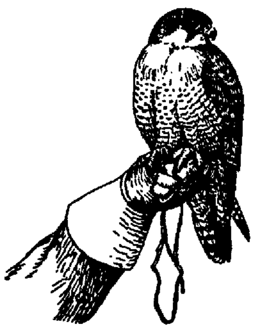
The early attempts to apply biology to the management of game as a wild crop soon disclosed the fact that science had accumulated more knowledge of how to distinguish one species from another than of the habits, requirements, and inter-relationships of living populations. Until recently science could tell us, so to speak, more about the length of a duck's bill than about its food, or the status of the waterfowl resource, or the factors determining its productivity. It is now become more realistic. Scientists see that before the factors of productivity can be economically manipulated, they must first be discovered and understood; that it is the task of science not only to furnish biological facts, but also to build on them a new technique by which the altruistic idea of conservation can be made a practical reality.

These, briefly, are the mental paths which led to the present

American idea of game management. The fact that hindsight shows them a bit crooked should not detract due credit from the pioneers who broke the way. There is no end to this path—our present notions will as surely be outdated as those which we here outdate. We seem due at this moment for a worthwhile advance. Both scientists and sportsmen now see that effective conservation requires, in addition to public sentiment and laws, a deliberate and purposeful manipulation of the environment—the same kind of manipulation as is employed in forestry. They are also beginning to see that in game, as in forestry, this manipulation can be accomplished only by the landowner, and that the private landowner must be given some kind of an incentive for undertaking it.

There are still those who shy at this prospect of a man-made game crop as at something artificial and therefore repugnant. This attitude shows good taste but poor insight. Every head of wild life still alive in this country is already artificialized, in that its existence is conditioned by economic forces. Game management merely proposes that their impact shall not remain wholly fortuitous. The hope of the future lies not in curbing the influence of human occupancy—it is already too late for that—but in creating a better understanding of the extent of that influence and a new ethic for its governance. Bailey (1922) says:

> "We are at pains to stress the importance of conduct; very well: conduct toward the earth is an essential part of it. . . . To make the earth productive and to keep it clean and to bear a reverent regard for its products is the special prerogative of good agriculture."



Chapter II

MECHANISM OF GAME MANAGEMENT

Productivity. In the light of this history, let us now examine the substance of game management itself. The previous chapter has traced the sequence of human controls brought to bear on the various factors which determine productivity. Just what are these factors? What are the characteristics of each? Which ones do we manipulate, and how? What is the effect of manipulation?

The concepts and definitions which spring naturally to the reader's mind will need only a little sharpening to suffice for present purposes.

Productivity may be defined as the rate at which mature breeding stock produces other mature stock, or mature removable crop.

In order to sharpen our mental picture of just what this means, we will have to employ figures.

Every wild species has certain fixed habits which govern the reproductive process, and determine its maximum rate. Thus bobwhite quail are monogamous, raise one brood each year after attaining the age of one year, and average 14 eggs per clutch, approximately half male and half female. Thus one pair of quail, if entirely unmolested in an "ideal" environment, would increase at this rate:

AT END OF	YOUNG	+	ADULTS	=	TOTAL
1st year	14	+	2	=	16
2d year	(16 ÷ 2)14 = 112	+	16	=	128
3d year	(128 ÷ 2)14 = 896	+	128	=	1024

This potential maximum rate of increase is, as nearly as we know, a fixed property of this species, and each other species likewise has its own fixed maximum breeding or reproduction potential. Thus antelope, which are polygamous, reproduce once each year from the age of two years, and average two fawns. Hence they could increase, during the same period of three years:

AT END OF		YOUNG	+	YEARLINGS	+	ADULTS	=	TOTAL
1st year		2	+	0	+	2	=	4
2d year		2	+	2	+	2	=	6
3d year	(4 ÷ 2)2 =	4	+	2	+	4	=	10

It is apparent, then, that the reproduction potential for quail is more than a hundred times greater than for antelope.

This maximum rate of increase is of course never attained in nature. Part of it never takes place, part of it is absorbed by natural enemies, and (on hunting grounds) part of it is absorbed by hunters.

Thus if, of the 16 quail present at the end of the first year, one-fourth were thereafter taken by hunters and one-fourth by other enemies, the increase would be:

AT END OF		YOUNG	+	ADULTS	=	TOTAL		HUNTERS		REMOVED BY OTHER ENEMIES		LEFT
1st year						16	−	4	−	4	=	8
2d year	(8 ÷ 2)14 =	56	+	8	=	62	−	15	−	15	=	32
3d year	(32 ÷ 2)14 =	224	+	32	=	256	−	64	−	64	=	128
								83		83		

On the other hand, if three-eighths of the quail were, after the first year, taken by hunters and one-eighth by other enemies, the rate of *increase* would be the same but the productivity, in the sense of crop removed by hunters plus the increment to the breeding stock, would be *half again as large.*

Productivity therefore differs from rate of increase, in that it includes increments to the removable crop as well as to the breeding stock. It is a better yardstick for measuring the condition of huntable game populations, which may not increase but which may nevertheless be highly productive in the form of hunting removals, or kill.

Productivity is something taken away from "other enemies" of game—a transfer of mortality from natural enemies to human hunters. It is actually, however, something more than that, because all of the stock may not breed unless its environment is favorable, and the creation of a favorable environment is the first concern of management. Management takes game away from other enemies and gives it to hunters, but it also creates otherwise non-existent game by allowing it to more nearly realize its breeding potential. This will be discussed later under "welfare factors."

Effect of Factors: Theory of Population. It is important to realize that no combination of factors ever occurs which enables game actually to increase at its theoretical maximum rate. Nevertheless the theoretical maximum is a convenient fixed datum by which diverse actual conditions can be measured and compared.

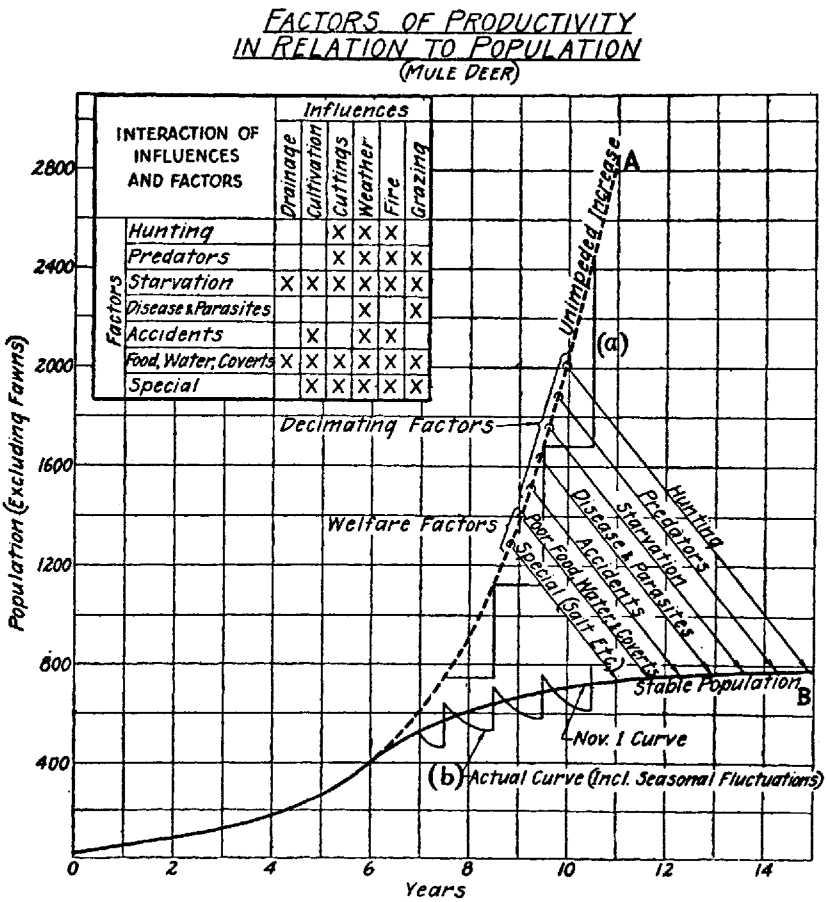
We may conceive, therefore, of population as a flexible curved steel spring which, by its inherent force of natural increase, is constantly striving (so to speak) to bend upward toward the theoretical maximum, but which the various factors are at the same time constantly striving to pull down. This conception is graphically represented in Fig. 2, in which mule deer are used as an example. In Curve *A* the initial stock is allowed an unimpeded increase, but in Curve *B*, after the sixth year, the increase is retarded by two classes of factors. One pulls down the curve by means of direct decimation, the other by retarded breeding. Their collective effect is to pull the ascending curve of unimpeded increase down to the usual actuality—a stable population.

The heavy lines *A* and *B* indicate the population from year to year if the census were taken annually at the season of maximum number of grown animals—say November 1. If the census were made each month, a zigzag curve, shown as a lighter line, (*a*) and (*b*), would result. With no mortality, these zigzags would be ascending steps with square corners (*a*). With normal decimation the zigzags are shaped like saw-teeth (*b*). In each case the vertical leg of each zigzag represents the yearly increment of young; the horizontal or descending leg the fortunes of the population for the remainder of the year.

For practical purposes it is of course unnecessary to take account of the zigzags in drawing population curves. What we want is trends, which the slope of the main curves adequately portrays.

The theory of population may be paraphrased in plainer language by saying that the capacity of game to increase or to produce removable surplus depends on the equilibrium between its breeding habits and the conditions under which it lives. The

FIG. 2



less unfavorable the conditions, the nearer the game comes to attaining the maximum possible increase or crop.

We classify the conditions into "factors of productivity" for purposes of analysis. Each factor is constant in character and direction, but not of course in value. It is the "values" which management seeks to control.

Chapman (1928) has called the summation of all the factors operating on any given population the "environmental resistance." Productivity is the breeding potential minus the environmental resistance.

The so-called "balance of nature" is simply a name for the assumed tendency of the population curves of various species in an undisturbed plant and animal community to keep each other horizontal. The growth of biological knowledge trends strongly to show that while population curves may oscillate about a horizontal median, a single curve seldom or never stays horizontal from year to year even in virgin terrain. Fluctuation in numbers is nearly universal.

A state of undisturbed nature is, of course, no longer found in countries facing the necessity of game management; civilization has upset every factor of productivity for better or for worse. Game management proposes to substitute a new and objective equilibrium for any natural one which civilization may have destroyed.

Classification of Factors. What we have called removals in these theoretical cases is, on actual game range, the sum of the toll taken by hunters, predators, starvation and drouth, diseases and parasites, and mechanical accidents. These we may call decimating factors because *they kill directly*.

There is another class of factors, which, like the decimating factors, were absent from our "ideal range," but which are always present in actuality. This second group includes non-lethal deficiencies of food, water, and coverts, and of certain special requirements such as salt, which will be discussed later. This second group, which we will call welfare factors, reduce productivity not directly by decimation, but *indirectly by decreasing the breeding rate and by weakening the defense against the decimating factors.*

There is obviously an overlap and inter-action between the decimating and welfare groups. Starvation and drouth are merely the acute stages of poor food and water. A mild degree of disease or parasitism does not decimate but merely reduces welfare. Furthermore decimating factors may affect productivity in other ways than killing. Hunters and predators may injure game without killing by driving it away from food or water, or they may by killing not only reduce the population, but also alter sex and age classes to the detriment of breeding. They may, on the other hand, benefit it in spite of decimation by scattering the game in such a way as to stock empty coverts or improve distribution, or by altering sex and age classes to the enhancement of breeding. Scattering may also benefit productivity by reducing contacts and thus checking diseases. Predators may reduce disease by removing weaklings.

By and large, however, the distinction between decimating factors which kill, and welfare factors which retard increase or make killing easier, seems a useful one, provided we bear in mind the overlaps and inter-actions between the two classes, and among the various factors in each of them.

There is a special group of welfare factors, part of which might be included under a broad definition of food, water, and coverts, but which are of sufficient importance in particular instances to warrant a separate category. They are here designated as "special."

This group includes gravel for gallinaceous birds and waterfowl, salt licks for herbivores and some birds, mineral springs for pigeons, dust baths for various birds, mud baths and hibernation places for bear, caves or dense shade for sheep and quail to reduce water loss during the heat of the day in arid climates, open wind-swept parks or deep water for the relief of moose and deer in fly season, and sandy knolls for "booming grounds" of prairie chickens. There are probably many other special factors we do not know about, and the ones we do know about may be more important than is commonly supposed.

There is reason to believe, for instance, that each species requires minute quantities of certain minerals, or certain protein vitamins. These are not "food" in the gross or quantitative sense. The quantities required may be so small that the amount transmitted from the parent to the egg seems in some cases to sustain the resulting progeny for a considerable period. Nevertheless they are so necessary that the exhaustion of the reserve supply in the tissues often results in malformation, impaired reproduction, or even death. The particular kinds of substances required by any given species does not seem to follow generic relationships; thus the requirements of hogs resemble those of chickens more than those of cattle. It is not unthinkable that the presence or absence of these substances helps determine the geographic distribution of species.

That a lack in the food, water, cover, or special factors actually decreases resistance to the decimators is well known. Thus deficient cover exposes game to hunters and predators; deficient food makes it unable to escape their onslaughts. Such deficiencies probably decrease the breeding rate in game, but this is not definitely established by actual proof in specific cases. It has long been observed, for instance, that during periods of drouth, Gambel quail coveys fail to pair off and nest. Apparently in such instances the disposition to breed is inactive for lack of some stimulus associated with normal weather, food, and cover, but the abnormal condition does not visibly affect the health of the adult birds. No one has proved that drouth is actually the cause of failure to breed, or through what deficit in food, cover, vitamin, or mineral it operates to this end.

Deficient food is also commonly believed to decrease the size or numbers of litters or clutches. In the Lake States, for instance, white cedar is an important winter food for deer when they are yarded up during deep snow. Yarding occurs during gestation. If a doe averages 1.5 fawns on a range well supplied with cedar swamps, she might average 1.4 fawns on a range from which the available cedar had all been cut for posts and poles. As will be shown later, such slight changes in the reproductive rate may have a profound effect on populations and productivity. No one has yet proved, however, that the doe: fawn ratio decreases with the available cedar.

Seton (1929) quotes R. MacFarlane as asserting that snowshoe rabbits have more and larger litters during the up-grade of the cycle. There is an unauthenticated report that the spruce hen in Nova Scotia lays a larger clutch of eggs before than after the cycle peak. It is also quite probable, though proof is lacking, that under an unfavorable set-up of welfare factors a part of the adult population may not breed at all. Just what welfare factors, if any, are associated with these highly significant changes in reproductive rate remains unknown.

While we lack proof that welfare factors change the breeding rate in game, they are known to do so in domestic stock. The probability that they do so in game is high enough to warrant the assumption for practical purposes.

To sum up, the factors of productivity overlap and interplay, but in their essential characteristics may be classified as follows:

DECIMATING FACTORS	WELFARE FACTORS
Hunting	Food supply
Predators	Water supply
Starvation	Coverts
Disease and parasites	Special factors
Accidents	

Influences. The reader may by now have noticed that this list of factors does not include certain environmental conditions known by all to affect game, such as drainage, cultivation, cutting and clearings, weather, fire, and grazing. These we propose to call *influences* rather than factors, because they usually operate on game indirectly by *influencing a factor*, rather than directly on the game itself. Moreover, they are sometimes favorable and sometimes unfavorable in their effects, whereas the factors are always unfavorable in being something less than ideal. Thus drainage does not kill game, but it alters food, water, and coverts, and thus welfare. Cultivation does not kill game, but it influences food, water, coverts, and special factors, favorably or unfavorably, according to the species, the circumstances, and the amount. The usual operation of influences is suggested by the table in the upper left corner of Fig. 2, the factors commonly influenced being indicated by "X" marks.

What we here desire to make clear is that any influence may usually be reduced to factors. The factors, then, are the *common denominators* of an infinite variety of influences, which condition productivity in all species of game at all times and places.

The particular set-up of factors here proposed may require modification with advancing knowledge; particularly with the further exploration of animal physiology and psychology. It will presumably always be true, however, that the thousands of environmental influences will be reducible to a small number of fundamental categories or factors which determine productivity, and that any kind of biological management will deal with their beneficial control.

Breeding Habits. The prospective field of opportunity for applying management to any given unit of population may be described in terms of Fig. 2 as bounded on its upper side by the unimpeded increase curve of the species in question, and on its

TABLE IA

BREEDING HABITS AND BREEDING POTENTIAL OF AMERICAN GAME BIRDS IN THE WILD

	1	2				3	4	5	
Species	Minimum Age of Bearing Young	Eggs Per Clutch (Min.-Max.) Aver.	Broods Per Year	Young Per Year	Mating	Females Served By 1 Male	Incubation (days)	Maximum Longevity (years)	Authorities (by columns)
Bobwhite Quail	1	(8-24) 14.4	1	14	M	1 (3 by forced mating)	23-1/2	10+	1,2,4,5,Stoddard; 3,Coleman
California and Valley Quail	[1]	(13-17) 15	(1-2?) 1	15	[M]	[1]	21-23		2, McLean,Grinnell; 4,Grinnell
Gambel Quail	[1]	(10-17) 12	1	12	[M]	[1]	21-24		2 ,Bailey,Grinnell,McLean; 4, Grinnell
Scaled Quail	[1]	(9-18) 13	[1]	13	[M]	[1]	21		2, Ligon; 4, Bergtold
Ringneck Pheasant	1	(7-16) 11.5	(1-3?) 1	11	P	(2-8?) 2	22	15,19	1,2,Wight,Grinnell,Beebe; 3,Beebe; 4,Grinnell; 5,Maxwell S.D. Game Dept.
Hungarian Partridge	1	(8-25) 16.4	1	15	M	1	21-24		1,2,3, Yeatter,Maxwell; 4,Bergtold Yeatter
Ruffed Grouse	[1]	(8-14) 11?	[1]	11?	P?	?	21		,2,Forbush,Grinnell; 3, Grinnell; 4,Bergtold
Blue (Dusky) Grouse	[1]	7	[1]	7	P?	?	About 21		,2,Ligon,Grinnell; 4,Grinnell
Pinnated Grouse	[1]	(7-17) 11.5	[1]	11	Pr?		(21-28?)-23		2, Bogardus,Gross; 3,4,Bergtold, Bogardus
Sharptail Grouse	[1]	(7-14) 12.4	[1]	12	Pr?	?	21-24		2, 3, 4, Grinnell, Schmidt
Sagehen	[1]	(7-9) 8	[1]	8	[Pr?]	?	22		2,Bailey,Grinnell;4,Grinnell
Whitewing Dove	[1]	(2-3) 2	[1]	?	[M]	[1]	18		2,Grinnell,Bailey; 4, Bergtold
Bandtail Pigeon	[1]	(1-2) 1	1	1	[M]	[1]	18-20		2,Grinnell; 4,Bergtold
Mourning Dove	[1]	2	2+	4+	M	1	About 14		2,Leopold; 3,4,Grinnell
Passenger Pigeon	[1]	(1-2) 1	(1-2?)1?	1?	[M]	[1]	14		2,Forbush,Barrows;4,Bergtold
Wild Turkey	2 (hens 1)	(10-18) 12?	[1]	12	P	4-5	28		1, 3, 4, Quarles; 2, Barrows 1, Randall.
Merriam Turkey	2	9-12	[1]	11	P	?	[26-28]		1,Ligon;2,Ligon,Bailey

Mallard	1	(6-15) 10	1	[10]	M or P	(3-5) 1	28		1, 2, Bent, Grinnell; 3, 4, Job, Grinnell
Blackduck	1	(6-12) 9	[1]	9			26-28		1,2,Bent,Grinnell; 4,Bergtold,Job
Bluewing Teal	[1]	(6-15) 11	1	11			21-23		2,Bent,Grinnell; 4,Bergtold,Job
Cinnamon Teal	[1]	(6-13) 9+	[1]	9+			21-23		2,Grinnell; 4,Bergtold
Greenwing Teal	[1]	(6-18) 11	[1]	11			21-23		2,Bent,Grinnell; 4,Bergtold
Baldpate	[1]	(6-12) 10	[1]	10					2,Bent,Grinnell
Shoveller	[1]	(6-14) 11	1	11	M?-!-	- 1?	28		2,Bent,Grinnell; 4,Bergtold
Gadwall	[1]	(7-13) 11	[1]	11			28		2,Bent,Grinnell;4,Bergtold,Job
Pintail	[1]	(6-12) 10-	1	9			22-23	13+	2,Bent,Grinnell; 4,Bergtold; 5,Lincoln
Canvasback	[1]	(7-9)	[1]	8					2,Bent,Grinnell
Redhead	[1]	(10-15)	[1]	12?			28		2,Bent,Grinnell;4,Bergtold,Job
Lesser Scaup	[1]	(6-15) 10	[1]	10					2,Bent,Grinnell
Canada Goose	2	(4-10) 6	[1]	6	M	1	28-30	50 200?	1,Job; 2,Bent,Grinnell; 3,Job; 4,Bergtold; 5, McAtee
Snow Goose	[2]	(4-8) 6	[1]	7?	M	1	26-29		1,3,Sutton; 2,Sutton,Bent, Grinnell; 4,Bergtold
White-fronted Goose	?	(6-7) 6	[1]	6	[M]	[1]			2,Bent,Grinnell;
Whistling Swan	2-3?(5?)	(2-7) 5	[1]	5	M	1	[35-40?]	100?	1,Bent; 2,Bent,Grinnell;3,Job; 4,Bergtold
Sandhill Crane	?	2	[1]	2			about 30	40?	2,Grinnell; 4,Bergtold
Wilson's Snipe	1(or 2?)	4	[1]	4	[M]	[1]	[20]		1,2,Forbush,Grinnell
Woodcock	1(or 2?)	(3-4) 3?	[1]	3	[M]	[1]	20-21		1,2,Forbush; 4,Bergtold

NOTE: Figures in brackets are assumptions.
Figures with question mark are backed by authority, but the writer doubts whether they are representative.
In the column "Mating," M = mongamous, P = polygamous, Pr = promiscuous.

Table IB

BREEDING HABITS AND BREEDING POTENTIAL OF AMERICAN GAME MAMMALS IN THE WILD

Species	1 Minimum Age of Bearing Young	2 Young Per Litter	Litters Per Year	Young Per Year	3 Mating	Females Served By 1 Male	4 Gestation (days)	5 Maximum Longevity (years)	Authorities
Cottontail Rabbit	[1]	(4-7)	(3-4) 3?	12?	Pr	?	30? 28?		2, 3, 4, Seton; 2, Lattringer; 4, Dice
Snowshoe Rabbit	1	(2-4) 2	2 sometimes	4?	Pr?	?	30?	7?	1, 2, 3, 4, Seton
Fox Squirrel	1	(2-4) 3	2 (in South)	6?	M?	1?		10	1, 2, 3, 5, Seton
Gray Squirrel	1	(3-5)	2 sometimes	8?	Pr	?	44	15	1, 2, 3, 4, 5, Seton
Whitetail Deer	2	(1-4) [1.5]	1	1.5	P	?	205-212	15	1, Lantz; 2, Newsom, Seton; 3, 4, Lantz, Shiras; 5, Lattringer
Mule Deer	2	(1-3) 1.5+	1	1.5+	P	?	195-210		2, Hall, Seton; 4, Hall
Columbian Blacktail Deer	2	(1-3) [1.5]	1	[1.5]	[P]	?	200		2, Seton; 4, Rampoint
Elk (Wapiti)	3	(1-2) 1	1	1	P	?	249-262		2, Roosevelt, Seton; 3, 4, Seton
Moose	2	(1-3)	1	[1.5?]	P	?	242-246		1, 3, 4, Seton; 2, Roosevelt
Woodland Caribou	?	(1-2) 1	1		[P]	?	217?		4, Seton
Rocky Mountain Sheep	3	(1-2) ?	1	[1.5?]	P	?	150?	20?	2, 3, 4, 5, Seton
Mountain Goat	2	(1-2) 1	1	1	M?	1?	180?	12?	1, 2, 3, 4, 5, Seton
Antelope	2 (or 3?)	(2-3) 2	1	2	P	?	245?		2, Seton, Skinner, Nelson, Roosevelt; 4, Skinner
American Buffalo	3	(1-2) 1	1?	1?	P		285	34	1, 2, 3, 4, 5, Seton
Black Bear	[3 or] 4?	(1-4) 2	1/2	1	M?	1	225	24	1, 2, 3, 5, Seton; 4, Skinner
Grizzly Bear	[2 or] 3?	(1-4) 2	1/2	1	M	1?	225		1, 2, 4, Wright; 3, Seton

NOTE: Figures in brackets are assumptions
Figures with question mark are backed by authority,
but the writer doubts whether they are representative.
In the column "Mating", M = monogamous, P = polygamous, Pr = promiscuous

lower side by zero or extinction. The point where management begins is where the pre-existing population curve enters the left side of this field. The objective of management is ordinarily to bend the population curve upward, or, more properly, to remove enough of the downward drag of the factors to allow it to follow its inherent upward trend.

Assume, for the moment, that the factors are under perfect control: how strong is this inherent upward trend, *i. e.*, how far upward can the population curve be bent? No further, in any case, than the unimpeded increase rate, which, as already stated, is determined by the fixed breeding habits of the species in question. Let us therefore determine and compare the breeding habits of the principal American species. From these we can later determine and compare their unimpeded increase rates, or breeding potentials.

Tables 1*a* and 1*b* summarize the information available on the breeding habits of our game birds and mammals respectively. Those who wish to check the derivation of the values may consult the explanatory footnote.[1]

Even the layman, however, should appreciate the paucity of our existing knowledge on some of the most fundamental breeding characters, and the comparative abundance of information on other characters of lesser importance. In species after species of birds the scientific literature offers the most minute descriptions of abnormally large or small clutches of eggs, without a word as to the minimum breeding age, or number of broods per year, or sometimes even the average clutch. This lopsided development is the subject of further comment in Chapter IV, as is also the detailed discussion of breeding characters of particular species.

Breeding Potential Chart. Having determined the breeding characters of the various species, we are now ready to classify and compare their unimpeded increase rates.

This rate, which we may call for short the breeding potential, depends *theoretically* on four properties:

1. The minimum breeding age.
2. The maximum breeding age.
3. The number of young per year, which is the product of the

[1] *Explanation of Tables 1a and 1b. Choice of Species:* Established exotics are included, as well as a few rare or extinct species representing some extraordinary breeding age, number of young per brood, or number of broods per year.

Evidence from captives is excluded except for incubation periods, size of mammal litters, and longevity of mammals. The first two characters are probably not affected by confinement, and in the last, except for rare banding records, no evidence exists except from captives.

Symbols. Figures in brackets are assumptions based on analogy with species in which the character is known. Figures followed by question marks are vouched for by authority, but the author questions whether they are representative. The expression (8–24)14.4 means, minimum, maximum, average. Decimal fractions in the average imply that an accurate determination has been made. The omission of any average means that the literature offers only maximum and minimum.

Variations in clutch or litter with favorable or unfavorable environment is unknown, and therefore ignored.

Authority. The numbers preceding the name of the authority in the column on the right refer to column numbers. Thus "1, 2, 4, 5, Stoddard" means that the figures in columns 1–2 and 4–5 are taken from Stoddard. The titles and dates of the particular publications are omitted to save space, but can usually be inferred by looking up the author in the bibliography (see Bibliography).

Computations. The column "young per year" is the average young per clutch or litter times the number of broods or litters per year. The figure ½ under litters per year means the species breeds only in alternate years.

number per clutch or litter times the number of clutches or litters per year.

4. The longevity beyond maximum breeding age (number of senescent or over-age adults).

This assumes a population perfectly balanced as to sex and age classes. If not so balanced, the breeding rate is further affected by:

5. The sex and age composition of the population.
6. The mating habits as related to that composition.

Any computation recognizing all these variables would be very complex. For practical purposes we may, however, obtain a useful comparison of breeding potentials by ignoring 2, 4, 5, and 6. For any short period 2 and 4 are inoperative anyhow. Moreover, in most actual wild populations, few individual animals survive long enough to pass beyond the age of breeding, and still fewer to die of old age. As to 5 and 6, our theoretical population is supposed to be perfectly balanced.

Let us, then, first of all classify the species according to the principal characters determining their breeding potentials, as shown in the preceding tables, namely:

1. Minimum breeding age.
2. Number of young per year.

This classification appears in Table 2. The important predators have been added for comparison. As indicated by the arrow, a position in the table near the upper right corner means rapid breeding; a position near the lower left corner means slow breeding. Doubts as to the position of certain species are explained in the footnote to the table.

Table 2 switches the light on some strange biological bedfellows, and on the mathematical reasons why they lie together. The lion and the lamb, for example, lie very close, both breeding (in so far as known) at three years, but the lion (cougar) leading by "half a cub." The goose and the wolf, the dove and the hawk, the squirrel and the fox, the rabbit and the cat, are neck-and-neck for breeding rate, and also prey-and-predator in their struggle for existence. The general trend, however, is for the prey to outstrip its predator in breeding potential. This is an ecological

TABLE 2

CLASSIFICATION OF SPECIES FOR BREEDING POTENTIAL

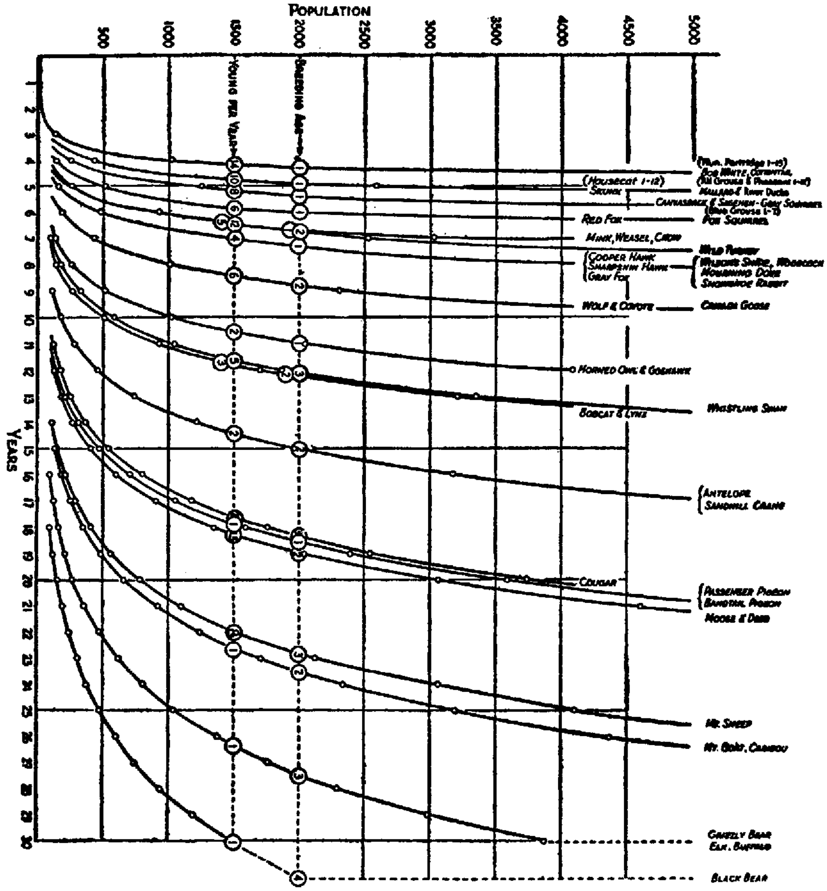
Breeding Age	Average number of young per year									
	1	1.5[12]	2	3	4	5	6-8	9-11	12-14	15-20
1 year	BANDTAIL PIGEON PASSENGER PIGEON[1]		Horned Owl Goshawk[2]	WOODCOCK[2]	MOURNING DOVE WILSON SNIPE[2] SNOWSHOE[3] Gray Fox Cooper's Hawk Sharpshin	Crow Mink Weasel	CANVASBACK BLUE GROUSE SAGE HEN FOX SQUIRREL[4] GRAY SQUIRREL[4] Red Fox	RIVER DUCKS SCAUP PHEASANT RUFFED GROUSE PINNATED GR. Skunk	BOBWHITE GAMBEL QUAIL SCALED QUAIL SHARPTAIL GR. REDHEAD COTTONTAIL[5] Housecat[2]	HUNGARIAN P. CALIF. QUAIL
2 years	MT. GOAT	DEER[6] MOOSE[6]	ANTELOPE[7]	Bobcat Lynx.			CANADA GOOSE Wolf[8] Coyote[8]		WILD TURKEY	
3 years	GRIZZLY[9] ELK BUFFALO[10]	MT. SHEEP[6]	Cougar			SWANS[11]				
4 years	BLACK BEAR[9]									

Low Potential — High Potential

CLASSIFICATION OF SPECIES FOR BREEDING POTENTIAL

1. May have nested twice
2. May not breed till second year
3. May have more than one litter
4. May have only one litter
5. Litters per year uncertain. Potential may be higher
6. Young 1-3, average about 1.5
7. May not always breed at 2 years
8. May breed at one year
9. Litter 1-4, average 2, breed only alternate years
10. May breed only alternate years
11. May not breed till 4th year
12. 1-2 or more young per year, averaging about 1.5

FIG. 3



principle, and is supposed to stabilize the animal community. If it were otherwise, the predator might the more often find himself in the predicament of John Burrough's potato-bug, which exterminated the potato and thereby exterminated itself.

The isolated position of certain species is worthy of mention. Thus the wild pigeons are unique in laying only one egg a year, and the woodcock in laying three. Odd numbers of eggs in the lower brackets seem to be rare. Here is possibly a problem for mathematical geneticists. The swan and turkey are unique in their deferred maturity; the bears in deferred maturity plus the peculiarity of breeding only in alternate years, which property makes the twin cubs average only one per year.

Breeding Potential Curves; Breeding Index. We have now determined the breeding characters of the species, and classified the species according to their two most important characters. Let us now take these two characters and compute and compare the resulting potentials.

The population tables resulting from these computations are for reference only, and are relegated to the appendix, Item *C*. From them the student may read at a glance what number (up to 5000) will result from any ordinary combination of characters in any short period of years.

Fig. 3 presents a graphic comparison of the unimpeded increase rates for certain typical species selected to show the effects of various combinations of breeding age and young per year. The position of other species in the general scale is shown by interpolating them at the top of the chart.

Each curve in Fig. 3 represents the plotted values which result from computing the increase determined by its minimum breeding age and young per year. These breeding characters are repeated, for convenience, in the two tiers of circles. Thus the first curve, which represents bobwhite, is marked 1 : 14, meaning "breeds at 1 year: averages 14 young." Any other species having the same index numbers would of course produce the same curve. The shape of the curve means that an initial pair could increase to 5000 in 4 years. On the other hand a pair of black bears, with the breeding index 4 : 1, would require over 30 years, or over eight times as long, to reach 5000.

The story told by Fig. 3 is a long one, not to mention the unanswered questions which it evokes. It tells us that starting with a single pair, our fastest breeders are capable of reaching 5000 in one-third the time that it takes for our slowest breeders to make even a perceptible start. It shows that *all* species have essentially the same type of curve, but differ only in the length of time it takes for the curve to approach the "straight up" trend. We have here a hint as to why small or thin populations are so much harder to build up than large or dense populations; also why the species capable of cyclic or irruptive behavior all lie toward the left or fast side of the chart.

A thoughtful examination of Fig. 3 also shows the extreme significance of minimum breeding age, and frequency of reproduction, as compared with size of the clutch or litter. These characters will be discussed in Chapter IV.

Our fastest breeders are the gallinaceous birds and cottontail rabbits, followed by river ducks, squirrels, wild turkey, snipe, dove, snowshoe, geese, swan, antelope, crane, pigeons, moose and deer, sheep, goat, caribou, grizzly, elk and buffalo, and black bear in the order named.

The smaller predators evidently breed nearly as rapidly as the gallinaceous birds, but the slowest predator (cougar) is not as slow as some of its antlered prey, or as the bears.

The slow breeding rate for bears arises from the assumption that cubs are born only in alternate years. Wright (1922) believes this represents the facts.

So much for the biological mechanism of population increase. It is one of those "scientific" subjects which cannot be concisely described except by means of tables and graphs, but the lay reader should not allow his unfamiliarity with these seemingly dry forms of expression to becloud his realization of the music inherent in their columns and curves. These are, in fact, the code symbols wherewith we may reconstruct the score of a great symphony. Education may be considered a success, and conservation an assured fact, when both layman and scientist can shift their attention from the symbol to the music—can hear with John Muir "every cell in a swirl of enjoyment, humming like a hive, singing the old new song of creation."

Limiting Factors. Having pictured the unimpeded increase rate inherent in the various species, we are now ready to consider further the factors which "pull it down" to actuality.

The classification of factors into decimating and welfare groups dealt with the *way in which* each factor pulls down the breeding potential. We have now to deal with the question, even more important from a practical standpoint, of the *extent to which* this is done.

The way, as we have already seen, is constant as to direction: all factors pull downward. The extent is exceedingly variable. It is determined by that whole vast and unstable gamut of circumstance which we call environment, and its interplay with the properties and also the numbers of a given species at a given time and place. This jig-saw puzzle is the province of the science of ecology. If the reader has never read a good text on ecology (such as Elton, 1927), he may here pause to do so, because game management, like every other form of land-cropping, is applied ecology. We can here cover briefly only certain ecological concepts, without which the succeeding chapters would lack meaning.

The most important of these is the concept of limiting factors. Of the nine factors operating on a given species at a given place and time, one often far outweighs all the others in the extent to which it pulls down the unimpeded increase rate. Where this is so, it may be called "limiting." Thus the Game Survey (1931) indicates that the limiting factor for quail on the corn-belt prairies is deficient winter cover, while in the dairy regions further north Errington (1931 *a* and *b*) has shown it is deficient winter food. It would do little good to feed quail in Iowa on an area in which the remaining winter coverts were already saturated, or to plant coverts in Wisconsin on an area bare of corn or weeds in winter. In neither case would the control of predators bring large returns, nor has the prohibition of hunting done so. The limiting factor is the one which *has to be moved first*, and usually the one to which the application of a given amount of effort will pay the highest returns, *under conditions as they stand.*

It should never be assumed, however, that the factor which is limiting at one time will remain so through any large degree of future change. For example: if food were augmented so as to fill up the Wisconsin coverts with quail, the lack of coverts would, from that moment, probably become limiting, and still more food would be as much beside the point as it is now in Iowa.

A limiting factor, then, is likely to remain limiting only through a rather narrow range of change. Some other factor will usually become the limiting one as soon as the original one is controlled to any great degree.

Game management consists largely of "spotting" the limiting factor, and controlling it. It also equally consists, however, in knowing when to stop, and what other factor next to turn to. It is as if the game manager's effort to "lift" the population curve were aided by "posts" of varying height, on which he may rest his burden provided he knows which post is most available for use at any given level, and provided he does not skip any posts in their ascending order of height, until he gains the desired elevation. (This analogy has its defects, but it may help dramatize the guiding principle.)

Limiting factors shift not only with the purposeful accomplishment of controls, but with accidental changes in weather or other environmental conditions. If the corn borer, for instance, should bring about the fall-cutting of Iowa corn, winter food would at once decrease to such an extent that the food factor would become the limiting one instead of cover, and the quail population would at once drop to the point where food and cover again balance.

Again, if a mild Wisconsin winter should accidentally follow a summer producing an extra heavy aftermath of ragweed on the stubbles, food might temporarily cease to limit quail, and the species would in the succeeding summer have a chance to increase up to the capacity of the coverts. This actually happened in 1932 following the mild winters of 1930–31 and 1931–32.

Another example: Stoddard determined that during the average year south Georgia quail are limited by food, by quality and distribution of cover, or by mammalian predators, the limiting factor depending largely on local variations in these conditions. However, coincident with the drouth years since 1928, there has been a rapid increase in fire ants (*Solenopsis geminata rufa*). This ant attacks the eggs at pipping time. The hen devours them as they come, but if the attack be too heavy, her defense is ineffective. They swarm into the pipped hole and soon reduce the chick to a tiny skeleton of dry bones, still entombed within the shell.

During the pre-drouth period these ants had destroyed only 4 per cent of the quail nests. In 1928 they destroyed 12¼ per cent. In 1931 they destroyed 12½ per cent in spite of control measures. It is not improbable that in badly infested localities, and during the present drouth, these fire ants, previously a minor component of the predator factor, have jumped into limiting status, due (presumably) to weather abnormally favorable for their increase.

Let the reader ponder the human as well as the biological import of these sudden shifts in factor values. They mean that the average values which characterize any given species in any given region are liable to unpredictable variations. The less the "spread" of factor values, the greater the probability of temporary shifts in the limiting factor. The less the spread, the greater the need for management accompanied by constant observational research, as distinguished from "rule of thumb" management based on some pre-determined formula. This is why a natural bent for research constitutes one of the personal qualifications for successful practice. Let the wielder of formulas stick to regions where the spread is so great as to minimize the probability of shifts.

To sum up: the whole field of environmental control consists, in short, of keeping the two most powerful factors in some degree of balance by controlling the one which pulls down the stronger. We control the stronger factor because it is the easiest way to raise the population curve one "step." There are shifts in factor values which the game manager must detect in time to shift his controls.

Effect of Controls. One more ecological concept will complete the reader's mental equipment for understanding the general mechanism of game management. He needs to know how extremely sensitive the population curve is. He must realize that environmental controls can be accomplished without completely rebuilding the face of the land. Often a very slight effort, skillfully applied at the right place, produces astonishingly large results.

It is difficult to give examples because in this country so little has been done, while in Europe more has possibly been done than was necessary.

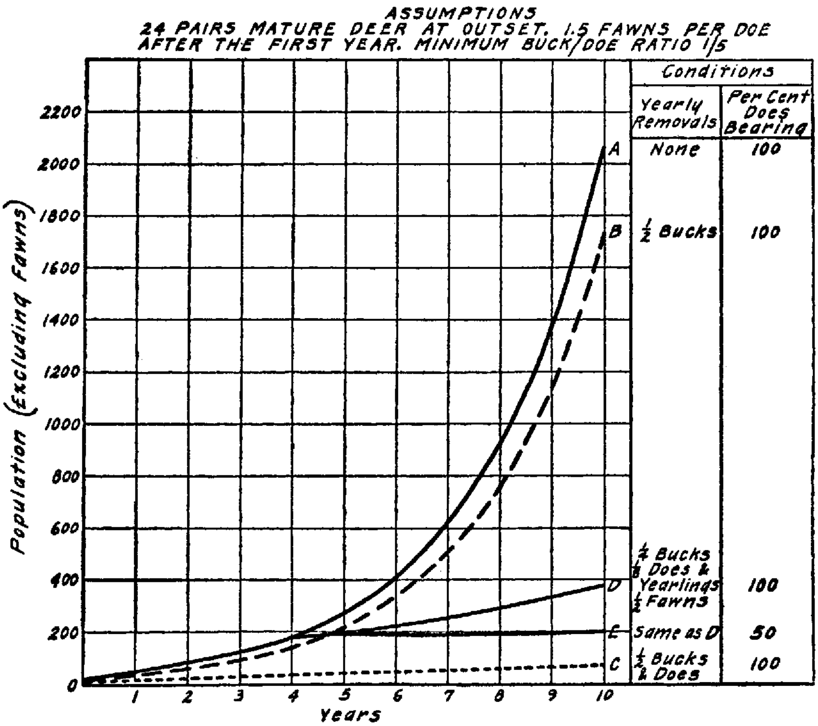
The overwhelming increase in Pennsylvania deer, for instance, was probably largely due to the partial control of the hunting factor through refuges, at a time when lumbering had left a large area of second growth offering excellent food and coverts.

In English grouse an increase up to 30-fold has been brought about through burning spots in the heather, partially removing old breeders, controlling predators, feeding grit, and draining wet places (Grouse Report). If the truth were known, it might show that the greater part of this increase came about through the first two controls alone, or possibly mainly through the first one, which brought about a diversification of the heather. Maxwell ascribes to the removal of old breeders alone (through driving) an increase of 300 to 800 per cent.

A theoretical example of the sensitivity of the population curve is shown in Fig. 4.

FIG. 4

SENSITIVITY OF POPULATION CURVE IN DEER



Curve *A* is the unimpeded increase for deer, beginning with 24 pairs.

Curve *B* results it half the *bucks* are removed yearly, beginning with the fifth year. Curve *C* results if, *from the outset*, half the *does and bucks* are removed yearly. Curves *B* and *C* contrast the perfect range closed until the deer get started, and then heavily shot under a buck law, with the same range shot from the outset to the same degree, without a buck law. This difference in management of herds *B* and *C* does not seem great, yet the *B* curve soars up toward almost unimpeded increase, while the *C* curve indicates bare survival.

Curve *D* results if, beginning with the fifth year, one-fourth of the bucks, one-eighth of the does and yearlings, and one-half of the fawns are removed yearly. This represents a range opened to bucks after the deer get started, but subject, in addition, to some law violation and moderate loss from predators. It is seen that the herd nevertheless increases. But if, in addition, half the does are barren after the fifth year, the herd declines as shown in Curve *E*. *D* and *E* contrast the degree of "punishment" a herd will stand as between (1) a favorable set of welfare factors bearing on the breeding rate, with moderate decimation, and (2) an unfavorable set of welfare factors depressing the breeding rate, and with the same decimation.

Fig. 4, while admittedly theoretical, is, except for Curve *A*, within the actual range of variation of the factors in actual deer country. It tells its own story of the potency of "management."

Game Farming. So far we have dealt with wild unconfined game populations, the mechanisms by which they are replenished, and the possible objective control of such mechanisms for purposes of sport and conservation. The breeding characteristics of species have remained fixed, because in wild game they cannot be greatly altered.

There is another kind of game management, however, in which not only the environment, but also sometimes the breeding rate, is subjected to control. Pheasants, quail, certain other gallinaceous birds, and also certain river ducks, when they are subjected to confinement and the eggs are collected as laid, may produce a number of fertile eggs far greater than the natural clutch. If these eggs are then incubated, artificially or by foster-mothers, a breeding potential curve may be attained which, in terms of Fig. 3, can only be described as "straight up."

A group of quail hens, for instance, has been known to lay 90 fertile eggs (or in one case, 128) per hen per year instead of 14, and pheasants 104 instead of 12. A usual figure for pheasants is 60 (McAtee, 1929*a*, and Simpson, 1927).

Game farming carries with this obvious advantage certain disadvantages which are well known. Complete confinement is expensive; the disease risk is increased by crowding; the resulting stock may lack, if later released, the sharp instincts conducive to wild survival. On vacant range, however, it is the obvious way to start an initial breeding stock, and on overshot range it is a feasible way of supplementing deficient breeding stock. We are not here concerned, however, with its costs, risks, or advisability, but rather with its fundamental difference from wild management, the latter regarding only environment as a variable, while the former regards both environment and breeding potential as variable and subject to control.

Summary. Game species differ enormously in their inherent breeding potentials.

In nature, no species realizes its potential, being held down by two kinds of factors. One kind decimates the population by direct killing. The other retards its increase by lowering reproduction and decreasing the resistance to decimation.

The factors interplay on each other, and are affected by numerous physical variables in the environment, such as weather and economic activities. These are called influences.

Productivity, or population increment, is determined by the equilibrium, more or less unstable, between the upward force of breeding potential and the downward forces of the factors. The downward forces, collectively, constitute the environmental resistance.

The breeding potentials of species differ greatly. For each species the potential is determined mainly by the minimum breeding age and the number of young per year.

Productivity is very sensitive to changes in the environmental resistance. The outstanding component in this resistance is called the limiting factor. Productivity changes whenever the limiting factor changes, and some other factor becomes limiting whenever any large change is made. Game management is the purposeful manipulation of factors.

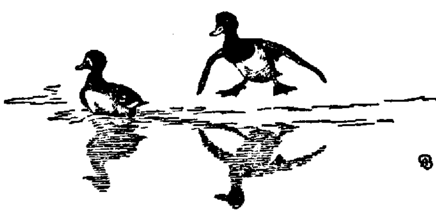
The spread of factor values may be large or small. Shifts in the limiting factor are more probable where the spread is small.

In artificial propagation, the factors are manipulated, as in wild management, but in addition, in some birds, the breeding potential is artificially increased.

This summarizes the primary biological mechanism on which game management seeks to exert a beneficial control.

To the lay reader its workings may seem obscure. If so, let him at this point turn forward to Chapter V on "Game Range," which describes in more detail the environmental forces to which the animal population must respond. Chapter V is not inserted at this point because the definitions in Chapters III and IV enter into its treatment.

To the scientific reader, on the other hand, this description of the biological mechanism may seem obvious. Let him pause, though, before he skips over it as redundant. We are depicting here the fundamental behavior of all aggregations of living things. Game management is only one of a thousand human activities, including sociology itself, directed toward the interpretation and government of that behavior. Civilization is, in its essence, the will to interpret and govern it.



Chapter III

PROPERTIES OF GAME POPULATIONS: FLUCTUATION AND DENSITY

The mechanism of management discussed in the preceding chapter applies to all species of game. Each species is governed by the same set of factors; each has a fixed wild breeding potential which the factors prevent it from attaining; each may be subjected to management by the same general mechanism of factor-control.

In the selection of controls, however, the game manager must take into account certain properties of game populations which are peculiar to certain species or groups, and others which vary so widely as between species or groups that they cannot properly be treated as a part of the common mechanism. This chapter deals with the little understood properties of fluctuation and density of populations. The next chapter will deal with the mobility and composition of populations, spread rates, tolerance to differing environment, to other species, to transplantation, and to domestication, and lastly the intricate phenomena of sex habits, sex ratio, sex balance, and flock organization.

Properties and Their Human Counterparts. Some of the important characteristics of various game species are already so well recognized that they need no particular comment. They have for years been the subject of investigation by naturalists and sportsmen, and are quite thoroughly recorded in the literature. These include the more obvious aspects of breeding habits and artificial rearing of game, movements in the sense of migration, gregarious phenomena (coveys, packs, etc.), food habits in the sense of average stomach contents, predatory enemies in the sense of their average food habits, and susceptibility to disease and parasites. The sporting qualities of various game species may also be mentioned as one of the recognized characteristics already adequately described by other authors. Some of these properties will be covered in Part II on "Technique."

This, however, by no means exhausts the list of characteristics important to game management. There are many others, and still additional ones no doubt await discovery. Many characteristics of game species are so manifestly a fixed attribute that they may, without unduly stretching the term, be called "properties," in the same sense that the specific gravity, or the coefficient of expansion, is a property of various chemical substances, or of industrial materials.

As in the case of *Homo sapiens*, some of the properties of game species are *not discernible in the individual* bird or mammal, but become apparent only through the study of the behavior of large aggregations of individuals, or game populations.

One of the most important properties of game populations, and one so far little explored, is the limit of density, or maximum number of individuals per unit area. This seems to apply to various groups of species in totally different ways. Since game management boiled down to its essentials is the control of game population density, it becomes apparent that an understanding of density limits is essential to successful practice.

Another property of great importance is the mobility of the individual, or the freedom with which the game population of a given area moves about within that area, or mixes with that of adjacent areas. This property may be measured through an indicator, which by analogy with the submarine or the airplane, may be called "cruising radius." The exploration of this property, through the technique of banding individual animals for later recapture, is just getting under way.

Another fundamental property is the tolerance of each species toward changes in the composition of its environment. This property in game is almost totally unexplored, but it is beginning to be evident that some species have a wide range of environmental tolerance, and others a very narrow one.

A fourth property, possibly compounded of the preceding three, is the minimum unit of range which any species can successfully occupy. Closely linked with this is the minimum number of individuals which may successfully exist as a detached population.

A fifth property, already well recognized, but by no means determined for the various species, is the tolerance of one species for another on the same range. While this property is usually thought of as a specific character, it seems probable that it varies with the population densities of the two co-habiting species, as well as with their respective habits.

A sixth property is susceptibility to transplantation, much written upon by laymen, but little understood even by scientists, let alone by those who risk their funds, or game, or lands in its exploitation. Many expensive failures in the importation of exotic species of game have emphasized the importance of this property. Other transplantations which were *too* successful are already well known.

Susceptibility to domestication, or breeding in captivity, is a seventh property which has long been the subject of experiment, and which has shown wide divergence among species and groups. It is now beginning to be appreciated that this property probably has its roots in some of the others already listed.

Lastly, each species and group has certain properties arising out of its sex habits and the composition of its populations by sex and age. That some species are polygamous and others monogamous has long been understood. In addition, however, it is now beginning to be recognized that some species or groups exhibit disturbances of the sex ratio by reason of disease or other factors as yet unknown, and that these disturbances are intimately connected with density limits and mobility. Disturbances of the sex ratio and age composition by hunting have long been recognized, but the limits beyond which such disturbances retard or enhance productivity are but dimly understood, and that only for a few species.

Cutting across many of these properties is the habit in many species of forming gregarious units. The existing literature tells which species form coveys, herds, and packs, and which do not, but it seldom suggests what these units consist of. The layman's assumption that each unit is a family is usually incorrect. A brief summary of what little is known about this question is a necessary basis for an understanding of management technique.

Does the lay reader, perchance, regard these "properties" as dry science, of small consequence to one who simply loves the living bird or beast? Let him pause before so deciding. "Love," if we mean by that word something more than mere reaction to hormones and instincts, implies an effort to understand. Can we understand wild things without understanding their properties?

The blind personification of animals, commonly known as nature-faking, arises from failure to face this question.

A little analogue with humans may add reality to the concept of properties. Man thinks of himself as not subject to any density limit. Industrialism, imperialism, and that whole array of population behaviors associated with the "bigger and better" ideology are direct ramifications of the Mosaic injunction for the species to go the limit of its potential, *i. e.*, to go and replenish the earth. But slums, wars, birth-controls, and depressions may be construed as ecological symptoms that our assumption about human density limits is unwarranted; that we may yet learn a lesson in sociology from the lowly bobwhite, which, as about to be pointed out in this dry chapter, "refuses" to live in slums, and concentrates his racial effort on quality, not ciphers. Where his racial exuberance gets the upper hand and causes him to depart occasionally from the rule, he suffers economic cycles and social unrest, and his civilization relapses to near-zero for a new start.

Bobwhite whistles merrily in spite of a low cruising radius. Gasoline has not lengthened his tether. But in his environmental and racial tolerances he is as finicky as any blue-stocking. His tolerance of transplantation is quite large, but his transplanters in their haste planted the wrong race. The outcome, hereinafter described, I will leave the Nordics to ponder.

Bobwhite's natural monogamy breaks down in the slums of the game farm. Whether his other properties still conform to "pattern" remains for science to determine.

I said that some properties are not discernible in the individual, but only in the mass. Need we go further than the various manifestations of mob psychology to prove that this is true?

Let us now return to our knitting: the more sober exploration of properties in wild species.

Criteria of Density. The yardstick wherewith we shall measure density is the number of individuals per unit area, but the reader should realize at the outset that this will carry us far afield. We shall encounter in some species a phenomenon called "Saturation Point" which seems to be a limit to the number of social units of fixed size, or coveys, per unit area. We shall see rhythmic density fluctuations in time, called cycles. There are other yardsticks which we shall not discuss, but only because we know nothing about them. Thus Elton (1932), after studying density in ants, advances the thought that the density of species should be compared not only in terms of number of individuals per unit area, but, if they differ in size, in terms of body-weight of populations per unit area. Does this acre support more *pounds* of ants than men?

This chapter deals only with the magnitudes and meanings of density measurements. The method of making them is covered in Chapter VI on game census.

Types of Population Curves. The limits of population density manifest themselves in at least three types of fluctuation as between years (see Fig. 5).

The first type is characterized by the absence of severe fluctuations. Such small fluctuations as occur from year to year may clearly be attributed to irregularities in visible factors, such as weather or predators. This mode of behavior of game populations seems in some birds to be associated with, or may even result from, the existence of a more or less fixed saturation point in number of head per acre. It may be called the flat type of population curve. It is found, for example, in southern quail.

The second type exhibits periodical oscillations of more or less fixed length and amplitude. Such oscillations are called cycles, and the species which exhibit them may be called cyclic species. It is found in northern grouse.

The third type of population curve exhibits severe but irregular fluctuations of no fixed length or amplitude. If these occur often, the curve may be called the fluctuating type; if seldom, it may be called irruptive. Lake States quail are irruptive.

For purposes of definition, fluctuations of over 50 per cent from average or normal density may be regarded as either cyclic, fluctuating, or irruptive, whereas population curves exhibiting fluctuations under 50 per cent may be regarded as flat. These definitions are arbitrary, and are inserted simply to clarify the ensuing discussion of density limits.

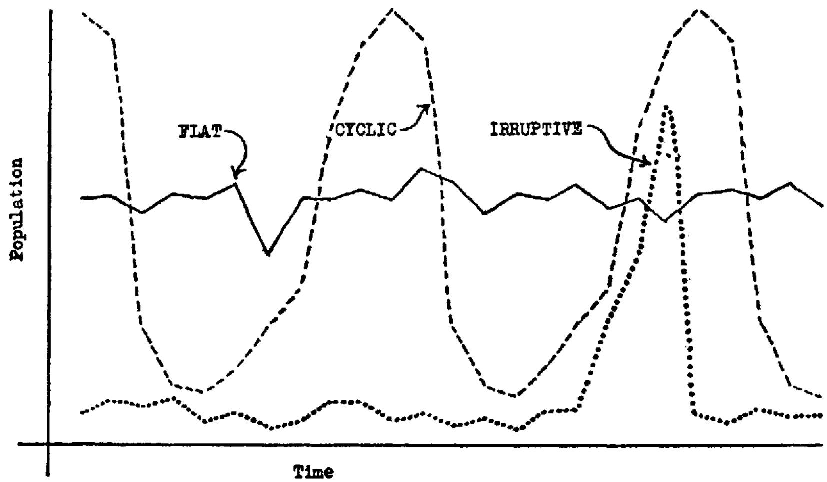
Saturation Point. When the maximum wild density of grown individuals attained by a species, even in the most favorable local environments, tends to be uniform over a wide area, that maximum may be called the saturation point of that species.

This is a different thing from the maximum density which a particular but less perfect range is capable of supporting. While this latter limit is literally saturation for that particular range, it is obviously a variable limit as between several ranges, and to avoid confusion, may better be called carrying capacity. A true saturation point occurs when a large number of widely separate optimum ranges exhibit the same carrying capacity.

It should be observed that while saturation point appears

FIG. 5

TYPES OF POPULATION CURVES



be a property of a species, carrying capacity is a property of a unit of range.

Every range has, of course, a limit of carrying capacity. Not all species, however, exhibit a saturation point. The existence of a saturation point is not yet definitely proved in any species, although I am personally satisfied that it exists in bobwhite. Stoddard, in the course of the Georgia Quail Investigation, first noticed that quail populations show an extraordinary reluctance to "pile up," even on seemingly ideal range, except for temporary periods of a month or so on small areas. In the Game Survey of the north central states (1931, p. 41), the various rough samples of quail populations throughout the region seem to be subject to an upper limit of one bird per acre, and the same limit was found in the separate game survey of Mississippi (unpublished) and Iowa (see Fig. 14).

Another significant indication was found during the Game Survey (p. 40) in Missouri, and later also in Iowa. The highest quail populations recollected by old-timers on their home farms in the early days of settlement fail to show any *former* populations in excess of a bird per acre. This indication, if substantiated by fuller data, means that the period of great abundance in quail, which is known to have occurred during the early days of settlement in the cornbelt region, consisted of a *higher proportion of populated acres*, rather than a higher maximum population per acre than now obtains.

Intensive management does not appear to break the quail saturation point, although of course it can increase the proportion of acreage attaining it. There are a few instances, however, in which management *seems* to have broken the saturation point. Thus M. E. Bogle obtained a population of seven quail per acre by intensive management on Round Island, Mississippi, but this density persisted for only one year. This island was three miles from shore and hence was practically a pen. It burned off during 1926, after which the project was abandoned. It is possibly significant that Stoddard found these Round Island birds infected with coccidia to an abnormal degree during this one year of extreme abundance. Even had the fire not occurred, the abnormal density might not have continued more than a short time.

There is, of course, a well-known tradition among sportsmen that quail populations are not susceptible of indefinite increase even under complete protection. Hundreds of writers have mentioned this, but few have interpreted it in a satisfactory way. The tradition probably reflects unsuccessful experience in attempting to break the saturation point.

While definite figures are lacking, there are, on the other hand, certain descriptions of bobwhite quail abundance in Oklahoma, Nebraska, and Texas which suggest the existence of natural unmanaged populations in excess of a bird per acre, at least at certain times in certain places. The possible significance of these exceptions will be considered later.

For the present it may be said with reasonable assurance that within the main range of the bobwhite, a density limit of approximately one bird per acre exists and probably always has existed.

Maxwell (1911) gives statistics on populations and kills of Hungarian partridge in England. His figures show a maximum kill of one bird per 2.3 acres during the best years, with a left-over stock of one bird per 1.5 acres. These figures taken together indicate a maximum density of approximately one bird per acre before the shooting began.

Maxwell says of red grouse in Britain:

"It seems there is some limit set to what a moor will produce, a limit not regulated by food-supply alone, and varying to a marked degree in different districts. Be the reason what it may, the fact remains that while on some exceptionally favored moors a bird to an acre may be killed in good years, others under the best management and most favorable conditions seem unable to yield a better average than one bird to every four or five acres."

A maximum *kill* of a grouse per acre, according to the conversion factor suggested in the Grouse Report, means a maximum fall population of roughly 1.5 grouse per acre, and a breeding population of a grouse per 2 acres.

In a mobile semi-migratory bird like grouse, temporary concentrations are especially likely, so that 1.5 grouse per acre may not have been resident on the particular moor, even though one per acre was killed.

Only one of the numerous specific kill records for red grouse given by Maxwell and the Grouse Report suggests a population over a bird per acre, but several approach it.

Maxwell gives the average kill of wild-raised pheasants on a 5,800-acre estate near London as 1,400, and the maximum as 2,000. This indicates a wild population of possibly one per two acres.

Figure 13 shows a pheasant census of 210 farms and a Hungarian partridge census of 54 farms within the established range of these species in Iowa. The maximum density of both species approaches, but in only one case exceeds, a bird per acre. This one case covers a winter concentration of pheasants known to be temporary.

My own combined evidence on the saturation point in bobwhite is this: 688 rough samples of bobwhite density gathered in the north central region during four different years show only one or two in excess of a bird per acre, and circumstances indicate these were temporary concentrations. Nineteen rough samples in Mississippi show only one in excess, and that was an island under intensive management, for only one year.

The evidence on the other game bird species mentioned is not regarded as anything more than indicative that they have limits and that the magnitudes are similar.

The evidence on density limits of mixed stands is presented in the next chapter in conjunction with that on inter-species tolerance.

To sum up my own present opinion on the saturation point: the laws of chance cause a large variation in the carrying capacity of local ranges. The laws of chance must once in a while produce a range approaching optimum, even where there is no management. Such accidental optima ought to show correspondingly high densities.

If external or environmental forces alone determined maximum density, the maxima occurring in a large number of samples in one state (or other large block) might be expected to run much higher or lower than in another. The fact that they do *not* run much higher or lower in bobwhite on its main range is evidence that some *internal* force or property, which is not subject to large variation as between regions, is also operative, and sets the upper limit beyond which wild populations do not increase.

Carrying Capacity. In hoofed mammals there is so far no visible evidence of any density limit except the carrying capacity of the food. This, of course, varies greatly between localities, and could hardly produce any such uniform upper limit as seems to exist in bobwhite. In New York John Burnham has for years carried 100 deer in an enclosure of 750 acres, or 7.5 acres per deer. Once when the herd was run up to 175 the vegetation showed prompt signs of trouble. Evidently 7.5 acres per deer is somewhere near the absolute carrying capacity of the food-bearing vegetation in that locality.

On the other hand the food-bearing vegetation of the Kaibab showed severe distress long before the (estimated) maximum of a deer per 40 acres was reached. The difference doubtless inheres in the semi-arid character of the Kaibab range.

The heaviest known deer densities in the wild, however, do not seem closely to approach the densities in confinement, even in similar country. Itasca Park, Minnesota (390 square miles) carried a deer per 32 acres in 1920; Grand Island, Michigan (22 square miles), a deer per 30 acres in 1923. The nearest approach to the Burnham density is Noah Major's estimate that Morgan County, Indiana, carried a deer per 16 acres in 1820 (Sandburg, 1926).

According to Clepper (1931) Pennsylvania is now carrying a deer per 12.5 acres of deer-supporting forest. This density is greater than Major's for Indiana, but since the Pennyslvania range is admitted by all to be overgrazed, its present deer population density is not considered a true carrying capacity. Clepper estimates that a density of a deer per 25 acres could be sustained, and that a deer per 40 acres would be conservative stocking. He compares the present Pennsylvania density to the following European densities:

	PER HEAD	
Roe deer in France	25	acres
Red deer in Bohemia	100	"
Deer, general limit considered safe	40–50	"

In the carnivorous predators there is frequent suggestion of a density limit, doubtless varying with locality, and possibly to be interpreted in terms of the territorial concept of Howard (1920), except that it holds yearlong. Jay Bruce, for instance, says that in California each cougar covers about three townships (see Boone, 1928). The old saying "one hill cannot carry two tigers" probably reflects an understanding of a density limit in large carnivores.

Whether there is in other mammals any saturation point, as distinguished from carrying capacity of the particular range, is totally obscure. One hundred twenty-two cottontails were trapped from a 35-acre island by the Pennsylvania Game Commission in 1930—a population of 3.5 per acre. A residual population of 50 was estimated as left, indicating that 5 rabbits per acre had probably been originally present. Hence, if there is any saturation point in this species, it is evidently much higher than in gallinaceous birds.

In the fenced rabbit warrens of England, where artificial winter feeding is practiced, a spring breeding stock of 6 to 8 rabbits per acre is recommended by Haddon (1931). This would mean a fall population many times as great, but the conditions approach those of domestication.

Let us now sum up the bearing of density limits on the expectations of management. In birds, until more is known about the subject, the game manager would probably be wise to assume that he cannot build up bobwhite quail or Hungarian partridge on large areas beyond a bird per acre (measured in the fall), and even this can be attained only on the most favorable range. In grouse the most that can be said is that there is no record of anything better. In pheasants higher populations were attained on rich land in Europe, even before the days of artificial rearing, and with such rearing are frequent there. In wild pheasants in this country, however, there is as yet no affirmative evidence of anything better, but there is a probability of it on certain extra rich ranges, such as parts of the South Dakota corn belt.

Nesting Densities. The apparent intolerance of continued concentrationwhich is here called the saturation point probably becomes operative under some particular set of circumstances, or at some particular season. One might guess from Howard's concept of "territory" that it became operative during the breeding season. If so, the maximum density of nests ought to show it.

Table 3 shows some instances of high nesting density in bobwhite and pheasant. The highest (6 quail nests on one acre, simultaneously occupied, and counted by Stoddard) may be ascribed to the fact that fire had concentrated the birds on unburned cover. The others may be regarded as normal maxima. They seem to approach or sometimes exceed a nest per acre.

Sprake (1930) describes two Hungarian partridge nests on one haycock, while the *Grouse Report* (p. 8) describes two grouse nests actually touching, and another nest incubated simultaneously by two hens.

While making the Game Survey of Iowa old-timers repeatedly described to me the great concentrations of prairie chicken nests which followed the prairie fires of pioneer days. Several said one could not walk across the unburned patches of grass without crushing chicken eggs "at every step."

These instances indicate that all upland game birds concentrate their nests under stress of necessity, and that none for which records exist display any intolerance of crowding great enough to explain the saturation point when their probable progeny is added to the adult population.

In short, the breeding season is evidently *not* the time when intolerance of concentration is most active.

Waterfowl seem to concentrate their nests even more freely

TABLE 3

HIGH NESTING DENSITIES

Species State	Acres	No. of Nests	Authority	Remarks
Bobwhite Georgia	1	6*	Stoddard	Concentration of nests after fire
Pheasant Pennsylvania	11	6	Pa.Game News	Exposed by mowing grass
South Dakota	15	10	Game Warden	Exposed by mowing alfalfa. June 1930
Iowa	10	13	J.F. Holst,Jr.	Exposed by burning winter wheat,1927.
Iowa	20	22	John Ball	Exposed by mowing alfalfa
Iowa	8	7*	Game Com.Release	Exposed by mowing clover

*Known to have been simultaneously occupied.

than gallinaceous birds. No nest counts that can be definitely related to a specified acreage are known to me, but a rough sample of nesting density may be interpolated from any census of ducks produced on a given breeding ground, provided it be taken early enough to avoid possible influx or efflux after the August moult or flightless period. Thus Day (1932, p. 10) says the Toussaint Marsh on Lake Erie, with an area of 1,500 acres, has produced each year for the past ten years from 10,000 to 15,000 ducks (black duck, mallard, pintail, bluewing). This means roughly at least two nests per acre, not deducting for blank acreage, which must be considerable in a marsh of that size.

On the 30,000 acres comprising the whole series of Lake Erie marshes Day says 200,000 ducks are produced, which means roughly a nest per acre, not deducting for a still larger proportion of blank acreage.

The *Game Survey* (p. 204) estimated a duck per acre produced on eight lakes comprising 9,600 acres in southwest Minnesota. These lakes were large and consisted mostly of open water blank for nesting purposes.

Density Limits and Fluctuation. Before discussing the probable significance of the known facts concerning density limits of species, it must be reiterated that science has hardly entered the threshold of this field of research, and that any and all generalizations possible at this time must have as their object the stimulation of thought rather than the promulgation of established truths. With this purpose in mind, it may be asked: What characteristics of the various species and their various environments seem to be associated with the three principal modes of population behavior?

First of all, how are cycles and saturation points distributed among the groups of species?

It is quite clear that cycles prevail in all species of American grouse, including ruffed grouse, pinnated grouse, sharptail grouse, spruce hen, blue grouse, ptarmigan, and possibly sage hen. In Europe red grouse and black game are cyclic. Cycles also prevail in the northern hares and rabbits in America, but not the southern ones. The western hares and rabbits experience violent fluctuations, but whether periodic cycles or irregular irruptions is not yet known.

On the other hand bobwhite quail and probably Hungarian partridges usually exhibit the saturation point.

Ringneck pheasants have the flat curve characteristic of saturation point species, but data on population density are too meagre to support any positive assertion for or against the existence of a saturation point.

The southwestern quails (gambel quail, valley quail, and scaled partridge) are known to exhibit violent fluctuations, but no work has been done to show whether these fluctuations show periodic cycles. It seems probable, however, that they are much less clearly cyclic than fluctuations in grouse. In a broad way we may say that cycles seem to be associated with grouse and rabbits, saturation points with bobwhite quail, Hungarians, and possibly pheasants, and fluctuations with other quails.

We are not justified, however, in stating that these modes of population behavior constitute properties of these generic classifications, because of the anomalous behavior of certain species *on the borders* of their ranges.

Bobwhites, for instance, on the northern border of their range in central Wisconsin, were found by the *Game Survey* (p. 43) to have exhibited radical fluctuations or irruptions. Another bobwhite irruption occurred in the wake of the Hinckley Fire in Minnesota in 1896 (unpublished), in northern Nebraska in 1880 (unpublished), and near Saginaw, Michigan, in 1863 (Mershon, 1923). Forbush (1912, p. 37) mentions two early fluctuations in New England, one of which (on Cape Cod) implies considerable density. These instances from New England and the Lake States clearly show a range boundary shifting with fluctuating density, but with one possible exception (Mershon, Michigan), no evidence of densities above the saturation point. For such instances we must turn to the Southwest. Wm. J. Tucker, state game commissioner of Texas, estimates more than two bobwhites per acre over several sections on the Norias Ranch, Kenedy County, in 1930. In 1923 a similar density, but including scaled quail, occurred over large parts of four nearby counties. Stoddard (1931, p. 500) quotes Starr as finding "more bobwhites than I ever saw before or since" in this same region in 1884. In Oklahoma, an old market shooter told Captain Charles Askins of taking 110 dozen birds off one quarter section, in 1904, in the Indian Nation. Askins found quail very abundant on this same locality in 1889.

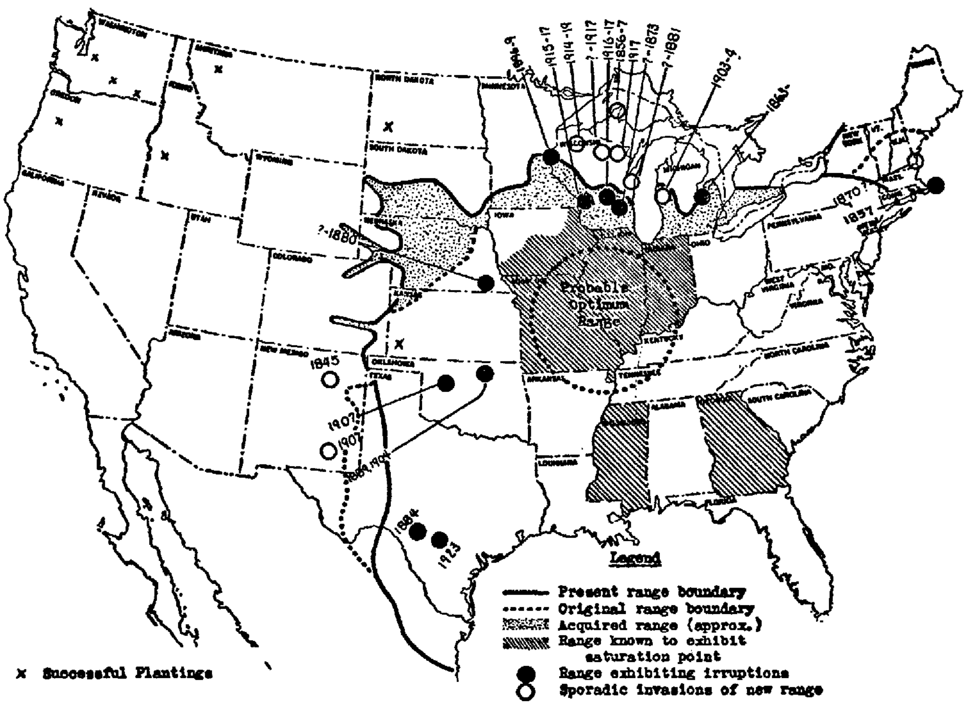
It would appear from these instances that on the northern and western borders of their range bobwhite quail fluctuate, and on the western border their density sometimes exceeds the saturation point. Some of these irruptions coincide with the grouse cycle (*Game Survey*, p. 78). The locations and dates appear in Fig. 6.

Conversely, the ruffed grouse which in its typical northern range is the most violently cyclic of any game bird, was found farther south to exhibit no visible cycle or fluctuation, past or present, in those small islands of grouse range which occur in Ohio, Indiana, Illinois, and southern Iowa (*Game Survey*, p. 151).

Observers in these localities who do not read widely do not know what is meant by a grouse cycle. In short, the ruffed grouse on the southern edge of its range seems to exhibit a flat rather than a cyclic population curve. An intermediate mode of behavior,

FIG. 6

FLUCTUATION OF BOBWHITE IN RELATION TO RANGE BOUNDARIES



Outline map, courtesy of Rand McNally.

consisting of a milder cycle than obtains in the north, was noted during the Game Survey in southern Wisconsin and southern Michigan. Prairie chickens likewise were found to show various transitions from a plain cycle in northern Wisconsin to a mild cycle in southern Wisconsin, and a flat or fluctuating curve in Indiana, Illinois, and Missouri.

From these observations the inference might be drawn that cycles are a property of latitude and longitude, and that all species tend to become cyclic in their northern or western ranges and flat in their southern or eastern ranges. That such an inference is incorrect is, however, clearly shown by the cyclic or fluctuating behavior of ruffed grouse in the southern Appalachians and in the Ozarks. C. G. Smith, in an unpublished report (1928) states that ruffed grouse were "innumerable" in the Pizgah National Forest, North Carolina, in 1920, numerous in 1921, and very scarce in 1923. Recent unverified reports of abundance in this region indicate a recurrence of the former behavior. Likewise in the Ozarks the Game Survey showed this species, which is now almost absent, to have been locally abundant in 1885, 1906, 1915, 1918, and 1926. These instances refute any fixed geographic distribution of cycles and saturation points, the bobwhite quail being clearly subject to the latter in the very regions (southeastern states) where the ruffed grouse is clearly subject to the former.

Geography of Cycles; Relation to Environment. It may next be asked whether the modes of behavior of game populations are induced by civilization, or whether they are inherent in the animal and the country. The probability that the saturation point always existed for bobwhite has already been explained. The conclusive answer to the permanence of cycles is found in Alaska and the Canadian interior, where violent fluctuations in grouse and rabbits are known to occur in an environment which, except for a few trappers, is as yet substantially unaffected by man.

The history of cycles likewise indicates that they predate radical modifications of the range by civilization. In Wisconsin the Game Survey traced evidences of temporary scarcity in ruffed grouse and prairie chicken back to 1881. King (unpublished) finds evidence of cycles in Minnesota back to the 1870s. Doctor Wm. A. Bruette has pointed out to me that the province of New Brunswick in 1814 closed the season on ruffed grouse, presumably because of scarcity. New York had a closed season as early as 1791. These early closures were, in all probability, periods of cyclic mortality. In the absence of more knowledge, we may therefore assume that cycles are inherent, rather than induced by civilization.

Another supposition, entertained in Europe, is that cycles are induced by the "artificial" conditions accompanying management. Leopold and Ball (1931*b*) have compiled records indicating severe fluctuations in red grouse in Britain as early as 1803, over half a century before any management began. It is also alleged that "keepering" has shortened the British cyclic period. Leopold and Ball find that back to 1858 the period has varied from 4 to 8 years, averaging 6.5 and showing no evidence of shortening. The kill curve on four grouse moors, which forms the basis for these conclusions, appears in Section D of Fig. 7. While the curve does not support the popular belief that management has shortened the cycle, it suggests a quicker recovery from depressions with the gradual inauguration of management since 1870.

Having concluded that the modes of population behavior are probably not an exclusive property of certain species, nor induced by civilization, it must follow that they are induced by some other property of the environment, and it remains to be seen what environmental characteristics are associated with each.

It is quite clear that cycles and other violent fluctuations are associated with adverse range (that is, cold, high, or arid range). This is the same as saying that cycles are associated with the periphery of the range of a species, because the distribution of the species stops where the environment becomes more adverse than its environmental tolerance can withstand. This would account for the anomalous behavior of bobwhite on the periphery of its range in the Lake States and the Southwest, and if we may regard some species ranges as all adverse, it would account for the behavior of the Southwestern species of quails, and the behavior of Canadian and Alaskan grouse and rabbits. The irruptions of Russian sand grouse, Scandinavian lemmings, and other foreign species tend to corroborate this peripheral-adversity hypothesis.

The *Game Survey* (p. 166) showed that pinnated grouse, on the range which they acquired through the invasion of the Lake States by agriculture, fluctuate more violently at the present time than they do on their original range in the prairie states, or than they did when they formerly existed there in large numbers.

This acquired range of the prairie chicken, being on poorer soil and farther north, may be considered as more adverse than the original home on the prairie, and hence corroborative of the "adversity" theory.

Cottontails likewise fluctuate on their acquired range in the Lake States (*Game Survey*, p. 95).

Adversity cannot, however, be the sole criterion, as shown by the behavior of ruffed grouse in the Ozarks and Carolina. These ranges are hardly adverse, but they are *large and continuous*. This suggests the further corollary that cycles are associated with large continuous blocks of range, as distinguished from small or discontinuous ones.

Certain other geographic peculiarities are worth mentioning, even though their interpretation at this time remains conjectural.

During the Game Survey of Wisconsin, a search was made for evidence of retardation of ruffed grouse mortality on the Door County peninsula as compared with the adjacent mainland. None was found. If cycles were due to an infection not previously existing in each locality, but spreading anew with each period of mortality, such retardation would presumably have been discernible.

The same supposition would lead one to expect that the dates of appearance of mortality when plotted on a map would show a zonal pattern spreading from centres of infection or foci. A map of the last cycle in Wisconsin, thus prepared by the *Game Survey* (p. 145), shows no zonal pattern, but on the contrary a completely irregular incidence, such as moths would make in invading a carpet. Recovery, however, sometimes exhibits geographic distribution. Thus in 1931 the recovery of all grouse in northwestern Wisconsin is much more complete than in northeastern Wisconsin.

While no evidences of a zonal spread-pattern were found in Wisconsin grouse, Elton (Matamek Conference on Biological Cycles, 1932) finds evidences of a zonal spread in Canadian hares. He finds that mortality in the MacKenzie valley started at the Arctic Ocean and spread southward, not reaching lower Canada until two years later.

The *Game Survey* also showed this geographic peculiarity: ruffed grouse are absent from a large proportion of the islands in Lakes Michigan, Superior, and Huron, even though these islands seem to offer suitable habitat. The smaller the island and the farther from the mainland, the less likely it is to contain grouse.

The geographic evidence so far available for North America, in so far as it can be interpreted at all, seems to fit four postulates, as follows:

(1) Gallinaceous game and rabbits are normally flat in the centre or optimum of their indigenous ranges, but tend to become cyclic or fluctuating as they approach the geographic limit of their distribution.

(2) When their distribution is artificially extended to acquired range, their population curves become more cyclic.

(3) Cycles are more severe on large continuous blocks of range than on small, dispersed, or discontinuous blocks.

(4) There is no evidence of zonal distribution of incidence, except possibly on very large areas.

An additional source of evidence is available in the history of cycles. The available data on history so far compiled will accordingly be summarized. The few scattered bits of history already cited are included in these compilations.

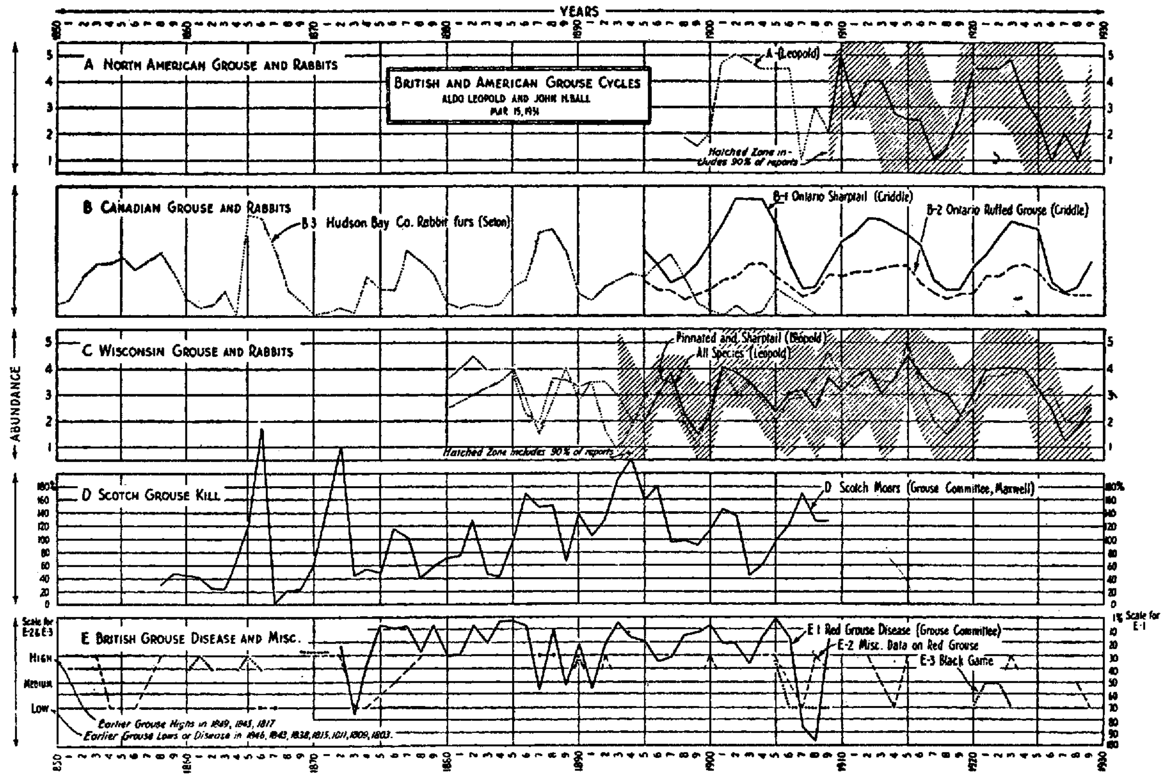
History of Cycles in America and Britain.[1] Fig. 7 gives a history of game cycles in North America and the British Isles. In interpreting the chart, the reader must keep in mind that most of the curves are summations of a large aggregate of local and variable conditions. Only curves *B*–1 and *B*–2 represent the behavior of game population in a single locality.

Curve *A* is the summation of some 540 reports gathered during the Game Survey on the status of various species of grouse and rabbits in various states and provinces during particular years. Some of the reports are from the literature, but most were obtained verbally or through correspondence from some 200 sportsmen, game wardens and naturalists. About two-thirds of these observations pertain to the northern United States and southern Canada, the remainder to the far North, the Rocky Mountain states, and the southern Appalachians. The vertical ordinate has no numerical validity, the curve simply connecting the most frequent of five grades of abundance reported as obtaining during each year. The hatched zone shows the "spread" of the 90 per cent of the reports nearest the median for each year.

The *B* curves are reproduced from the publications of Criddle (1930) and Seton (1923). Criddle estimated the number of grouse on his farm at Aweme, Manitoba. Seton compiled the records of

[1] This material was published by Leopold and Ball in *The Canadian Field-Naturalist* September, 1931, under the title of "British and American Grouse Cycles."

FIG. 7



YEARS
ABUNDANCE
A North American Grouse and Rabbits
British and American Grouse Cycles
Aldo Leopold and John N. Ball
Mar 15, 1931
A (Leopold)
Hatched Zone includes 90% of reports
B Canadian Grouse and Rabbits
B-3 Hudson Bay Co. Rabbit furs (Seton)
B-1 Ontario Sharptail (Criddle)
B-2 Ontario Ruffed Grouse (Criddle)
C Wisconsin Grouse and Rabbits
Pinnated and Sharptail (Leopold)
All Species (Leopold)
Hatched Zone includes 90% of reports
D Scotch Grouse Kill
D Scotch Moors (Grouse Committee, Maxwell)
E British Grouse Disease and Misc.
E-1 Red Grouse Disease (Grouse Committee)
E-2 Misc. Data on Red Grouse
E-3 Black Game
Scale for E-2 & E-3
High
Medium
Low
% Scale for E-1
Earlier Grouse Highs in 1849, 1845, 1817
Earlier Grouse Lows or Disease in 1846, 1843, 1838, 1815, 1811, 1809, 1803.

the Hudson Bay Company showing their purchases of rabbit skins.

Curve *C* was obtained during the Game Survey of Wisconsin. It is a summation of data similar to but separate from Curve *A*. The hatched zone represents the spread of 90 per cent of the reports.

Curve *D* is the kill of red grouse from four Scotch moors as published in the Grouse Report, and by Malcolm and Maxwell (1910). The curve represents the departure from average (100 per cent) of the four moors collectively. The rising trend of the curve represents the increasing success of management.

Curve *E*–1 is an inverted frequency curve of the reports of disease in British red grouse as mapped by years in the Grouse Report. The curve is plotted as the departure from average of the total number of reports of disease for each year.

E–2 is a compilation of textual references to high and low red grouse crops, kills, bags, and disease years in the Grouse Report, in Malcom and Maxwell, and in a paper by MacIntyre (1930). The vertical ordinate represents an arbitrary judgment, in three abundance classes, on the consensus of textual references available for each year. *E*–3 consists of fragments of textual references to high and low years in black game by the same authors.

The North American grouse curves (but possibly not Hudson Bay rabbits) substantially synchronize in their fluctuations back to the high of 1902, at which point the data become too meagre for further comparisons. The periods and intervals are:

NORTH AMERICAN GROUSE CYCLE

Interval		10 or 11 years		10 or 11 years		
High	1902		1912 or 13		1923	
Low		1906		1918		1927
Interval			12 years		9 years	

Evidently 2½ cyclic periods elapsed between 1902 and 1927, which gives an average period of a fraction over ten years.

Seton likewise deduced a ten-year period from his Canadian curves for rabbits and fur-bearers. Since he covers an earlier and nearly separate history, it would appear that the American cycle is not changing in length. It is not here intended to imply that it has or has not a uniform period. An average is needed in any event for predictions in game management and administration.

The British curves likewise seem to show more parallelism than would occur by chance alone. The disease curve *E*–1 should precede the kill curve *B* in both trough and peak, because disease is usually noted a year or two before the population and the kill begin to fall off. This anticipated lag is often apparent on the chart. An analysis of the British grouse curves indicates that seven periods have elapsed between 1863 and 1908, ranging in length from four to eight years, and averaging 6.5 years, which is a close approximation to the "seven year cycle" of tradition.

Since America and Britain seem to have cyclic periods of different length, the occasional synchronism between them on the chart must be ascribed to chance alone.

We may draw from these historical studies the following additional postulates:

(5) The length of the cycle period in North America averages about ten years, and is apparently somewhere near synchronous in the various parts of the continent.

(6) The length of the cycle period in the British Isles averages about 6.5 years, and is somewhere near synchronous in its various parts, but (as is evident from its length) not synchronous with the North American period.

Fur-bearers and Small Rodents. To this list of tentative conclusions the Matamek Conference on Biological Cycles, and Elton (1931) have added three more in part entirely new:

(7) The fur-bearers of Canada in general share the grouse and rabbit cycle, except that the muskrat cycle is inverse to it.

(8) The lemmings and arctic white foxes of the American arctic show a four-year cycle.

(9) Salmon and cod on the Atlantic coast of Canada seem to share the grouse and rabbit cycle.

Possible Causes of Cycles. None of the foregoing speculations deal with causes.

The cause or causes of the wild life cycle are unknown, but the nine postulates drawn from its behavior in time and space at once narrow the possible field of speculation. The seeming synchronism of cyclic phenomena, if not refuted by data from new regions, makes it necessary to postulate some cause operating simultaneously over the whole continent. Fluctuations in solar radiation, in electro-magnetic conditions, or in some other cosmic force might meet this specification.

Such a force, however, cannot directly kill grouse, or rabbits, or fish. It must either activate some lethal factor, such as disease, or change some welfare factor, such as food, or else change the breeding potential by some physiological influence as yet unknown. Such a force might conceivably do several of these things.

Because of the sudden nature of the decimation in grouse and rabbits, and the fact that numerous sick and dead individuals are found during the "crash," the most likely hypothesis in the case of these animals is that the assumed cosmic force operates through the agency of disease. It might operate by (1) decreasing disease resistance in the host; (2) increasing the virulence of disease organisms.

Green's hypothesis (*Matamek Conference on Biological Cycles*, p. 11) explains how virulence in a bacterial disease, such as tularemia, might fluctuate rhythmically without the intervention of any cosmic force. The recent trend of the pathological evidence favors bacterial or virus disease, rather than parasites, as the primary lethal agent in grouse and rabbits, and varying virulence, rather than varying "resistance," as the determinant of mortality. To complete this chain of theory, it is only necessary to assume that Green's virulence-rhythms are in some way *synchronized* by the cosmic force. Just how this might happen is still "beyond our depth."

Since the formulation of Green's hypothesis, his own findings tend somewhat to weaken some aspects of it. It should be weighed in conjunction with these later and as yet unpublished findings.

We may label the above presentation as the "radiation-virulence" theory. It leaves the fish cycle unaccounted for; also the anomalous behavior of muskrats and the short cycle of arctic foxes.

The other possibilities, however, should not be left out of account. Irradiation of foods, kinds of food as affected by weather, or reproductive rate as affected by food, or by radiation directly, may be secondary causes, or they may be primary, with disease playing a secondary rôle. In any event parasites certainly play an important secondary rôle (see various publications of Gross and Allen), or even a primary rôle in some regions (Grouse Report) as well as predator migrations arising out of the disappearance of buffer foods (Burnham, 1918).

Function of Cycles. Cyclic phenomena are most strongly associated with northern animals either possessing specialized digestive capacity for living on low-grade foods (buds and bark), or preying on others that do.

Ability to live on low-grade foods means immunity from winter starvation.

Saturation phenomena, on the other hand, are most strongly associated with less specialized birds depending on seeds for winter survival, and hence not immune to winter starvation.

The simplest inference is that the function of cycles is to hold within bounds those species which might otherwise, by reason of their immunity from starvation, increase to the point where they would devegetate their own range.

The overlaps between the two alternative modes of density control are harder to interpret. Quail and cottontails may be cyclic on their range peripheries because they are there heavily exposed to the cyclic diseases of grouse and hares. Why the small islands of grouse show a flat curve in the south remains, however, an enigma. Possibly their isolation, or the absence of carriers, has something to do with it.

Cycles and Management. (See Leopold and Ball, 1931*a*.) Many game conservationists have been skeptical about the feasibility of applying management to American grouse, especially American prairie chickens. The violent fluctuations comprising the cycle have been regarded as making the potential crop uncertain, and efforts to produce a crop correspondingly unattractive.

This attitude seems unjustified. Grouse management in Britain is universally regarded as a success. That property in grouse which causes them to fall ready victims to disease epidemics is apparently offset by a corresponding facility in recovering from their effects.

The first thing which a prospective manager of grouse wants to know is what proportion of the years must be expected to show crop failures. The bag on the four moors covered by Curve *B*, Fig. 7, fell lower than 50 per cent of normal or average during only 14 years out of the 51-year period covered. Crop failures in Britain, accordingly, seem to occur during only one year out of four on the average. This is under management. No comparable figures are available for the unmanaged grouse populations of America.

The British curve gives some indication that management, which began about 1870, has shortened the periods of depression, *i. e.*, has speeded recovery from the cycle. What management has done in Britain could presumably be repeated here.

A less direct indicator of the feasibility of management is the maximum fluctuation from normal. This in Britain often exceeds 90 per cent of the average, as measured by the kill. Probably the fluctuation in actual population density is as great or greater. There are as yet no comparable American figures on degree of mortality, but the British figures agree substantially with the conjectures advanced in the Game Survey for ruffed grouse and rabbits. For Wisconsin prairie chickens it was conjectured that the fluctuation did not often exceed 70 per cent.

There is no convincing evidence of just what increase in red grouse has been accomplished by management in Britain. Maxwell doubts whether there has been any increase in the highlands of Scotland, but in England he asserts there has been a 300 to 800 per cent increase, and he ascribes it to a single aspect of management, namely "driving." One may be entitled to doubt whether this increase has been accomplished by driving alone. It seems logical to ascribe it to the environmental controls which began at the same time as driving, as well as the alterations in sex and age classes accomplished by driving itself. These will be discussed later.

The general consensus of the evidence is that there is an unutilized and attractive opportunity for applying management to American grouse, especially prairie chickens, these being a close analogy to the red grouse of Britain, in which management has so far been an undoubted success.

Summary. Game populations display certain limits of density and certain fluctuations in time which are of great import to management, but as yet not understood.

Bobwhite shows an upper limit of density of about one bird per acre called the saturation point, which holds good over most of its geographic range. It seems to be a fixed maximum for the highly diverse carrying capacities of local range units. It is associated with a flat population curve.

American grouse, hares, and rabbits show a cyclic population curve of 10-year period, but no visible saturation point.

On the peripheries of their geographic range, however, quail show the fluctuating curve of grouse while in their former centre grouse show the flat curve of quail. It may be inferred that cycles and saturation points are alternative modes of regulating density, the former prevailing in adverse peripheral environments and the latter in favorable or central environments. Continuity in habitable range also seems to favor cycles.

A similar cycle of lesser length (6.5 years) prevails in British red grouse. Management has not changed its length or amplitude, but it has shortened the intervals of scarcity by offering favorable conditions for recovery of normal numbers.

Cycles, and possibly also saturation points, are caused by disease. The variant is probably the virulence of the disease organism. The fact that the cyclic period is substantially synchronous over this continent indicates that the virulence may be affected by some cosmic force as yet unknown.

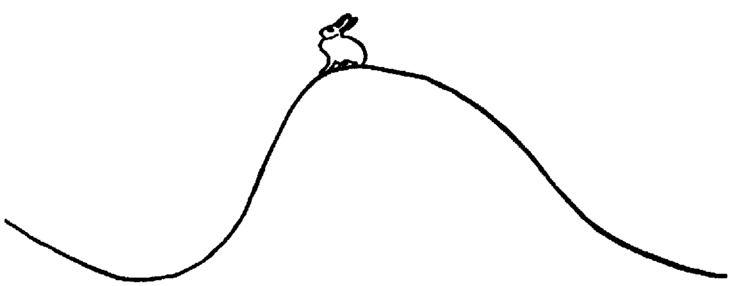
Cycles are most pronounced in species which are immune to starvation because of their food habits, or which prey on such species. Their function is to prevent such species from devegetating their range.

This account of what little is known, or guessed at, about fluctuation and density limits in game, contains a high percentage of surmise or speculation, because the accumulated labor of naturalists contains a low percentage of attention to this fundamental subject. Scientists have been studying it in the handmade glass-bottle environments of the laboratory. This is proper —they will some day extend their controlled experiments to the hills and fields. But the game manager faces it here and now. If he is possessed of that curiosity which insists on finding causes for the "acts of God," this chapter may help his search.

It is unlikely that any game manager will find the explanation of cycles, but his field observations are the main reliance of the scientists who will.

That man is unimaginative indeed who can regard these mighty pulsations in the wild life of whole continents without seeing that the myriads of living things which constitute the biological community are a living organism with an entity of its own, as interdependent and co-operative in its parts as his own body.

Trying to understand its workings is a worthy calling; saying that one does understand it is another matter, a mere "voice, audible for a moment in the derisive silence of eternity."



Chapter IV

PROPERTIES OF GAME POPULATIONS: MOVEMENTS, TOLERANCES, AND SEX AND FLOCK HABITS

MOVEMENTS

Radius of Mobility. If a crop of game remains on the farm where it was raised, the incentive to produce it is operative for individual farmers. If, on the other hand, the game wanders over several farms, the owners must organize as neighborhood groups in order to make management fully effective. In other words, the mobility of the species determines the minimum unit of management.

How far a game refuge will feed breeding stock to a surrounding hunting ground determines the size and frequency of refuges needed. The answer again depends on the mobility of the species.

These are simply two examples which show why the property of mobility, or length of cruising radius, is of fundamental importance in selecting a scheme of management.

Mobility varies greatly as between species. The yearly mobility may be almost zero in quail, but almost half the circumference of the earth in certain migratory birds like the golden plover or the arctic tern.

The recently developed technique of bird banding has shown a considerable variation in mobility as between individuals, and between the sex and age classes of a species, but it remains true that each species has a characteristic range of variation which differs from that of others, and which may accordingly be considered to be a property of that species.

The various groups of species display some internal similarity in this property. Thus all the ducks are mobile, while none of the hares and rabbits appear to be so. Some groups, however, display internal variations. Thus ruffed grouse are non-mobile, while red grouse are mobile, and pinnated grouse are semi-migratory. Whitetail deer are non-mobile, while mule deer perform considerable migrations.

Almost all of the banding work to date has been done on migratory birds. Non-migratory birds and mammals are as yet almost untouched. Accordingly it is impossible in the case of many species to give detailed figures, or even to compare one species with another.

In any comparison of mobility as between species, the unit of time must be taken into account. The daily radius, the radius as between seasons, the annual radius, and the lifetime radius may each be an entirely different thing.

Within a given species the environment must also be taken into account. Elton (1930) thinks that a sense of disharmony with environment tends to stimulate movement. Overpopulation, weather, activity in the decimating factors, or deficiency in the welfare factors probably stimulate it. These are all temporary disturbances of the environment. Possibly certain adverse environments are so constantly disturbed that mobility is permanently stimulated. In quail, for instance, there is reason to suspect that annual mobility increases toward the edges of the geographic range.

It has already been noted that quail, and possibly other species, tend to become cyclic toward the edges of the geographic range. Fluctuation in population and free movement of populations seem to go together in the gallinaceous birds (but not in waterfowl or mammals).

Likewise the opposite properties of saturation points and low mobility tend to be associated.

There is possibly some connection between the property of population limits and that of mobility, although its nature is yet to be explored.

The only adequate study as yet made of the mobility of any non-migratory game bird or mammal is the Georgia Quail Investigation. Stoddard (1931, p. 175) banded 1410 bobwhites in spring during two successive years on two plantations. Within three years he had recaptured 200 of them, either by retrapping or by finding them in the bags of shooters. Table 4 gives the frequency of the various distances between the point of banding and the point of recapture.

The frequency of the time intervals between banding and recapture was: after first breeding season but before the second, 77 per cent; after the second but before the third, 17 per cent; after the third but before the fourth, 6 per cent.

The substantial parallelism in results between the two different locations studied makes it safe to conclude that on the Georgia preserves nearly half the quail spend their life-span within a quarter-mile of their birthplace, while few ever wander more than a mile. Individuals, rather than coveys, are the unit of movement. One covey moved as much as a mile intact, but the great bulk of the movement occurred by the shifting of individuals as

TABLE 4

YEARLY MOBILITY OF BOBWHITE QUAIL

Georgia Quail Investigation

No. Banded Place Time	No. of Banded Birds Shot or Retrapped	Distance from place of banding, Miles 0-1/4	1/4-1/2	1/2-1	Over 1
1,051 March-April 1925 & 1926 Forshala Plantation	135	46%	35%	15%	4%
579 March-April 1925 & 1926 Melrose & Pebble Hill Plantations	65	52%	17%	12%	18%
1,410 (Total)	200	48%	29%	14%	9%

between coveys. There was no significant difference in mobility of the sexes.

Errington's more limited banding of quail in Wisconsin corroborates Stoddard's findings, but he found little movement of either individuals or coveys in midwinter, except under stress of starvation.

This roughly expresses the season, yearly and lifetime mobility of bobwhite on two opposite ends of its range. There is no reason to believe it is much different elsewhere, except during the peripheral irruptions described in Chapter III.

As to daily mobility, banding is not conclusive, since individuals are rarely or never captured twice the same day. It may be safely said that daily mobility is always less than seasonal, and always less in the nesting season than at other seasons. Stod-

Table 5

COMPARATIVE MOBILITY OF GAME SPECIES

(Banding records considered representative are in plain figures. Opinions are enclosed in parenthesis. Exceptional banding records on single individuals are enclosed in a circle.)

Species	Observer	Daily radius, miles		Yearly radius, miles	
		Average	Maximum	Average	Maximum
Bobwhite	Stoddard, Georgia	1/8	1/4	1/2	3 ⑦
	Errington, Wis.	(1/4)	3/4-1 3/4)		
Valley Quail	Price, California (Condor, Jan. 1931)	1/4	1/4	1/4	1/2
Ringneck Pheasant	Wight, Michigan	1/8-1/2	2-3	1/2-1	6
	*Ely, Pa.				㊵
	*Leffingwell, New York				2 ⑥
	Thomas MacClure, England				(2-5)
Hungarian Partridge	Thomas MacClure, England				(1/3-1/2)
	Yeatter, Michigan	(1/8)	(1/2)	(3/4)	(3)
Ruffed Grouse	King, Minnesota	(1/8)	(1/2)		(2)
	Gross, New England	(1/4)	(1)		
Prairie Chicken	Cooke, Iowa (1888, p. 105)				(200?)
Sharptail Grouse	Schmidt, Wis. (unpubl.)	(1/2)	(2)	1	3
Red Grouse	"Grouse in Health & in Disease"				(20-30)
(England & Scotland)	Malcolm & Maxwell		$1\frac{1}{2}$?		
Elk	Rush, Sun River Herd	(1/2)	$(1)^x$	(15)	(35)
	Rush, Yellowstone Herd	(1/2)	$(1)^x$	(45)	(120)
Mule Deer	H. C. Bryant, Calif. Jour. Mam. Aug. 1924				⑳
	McGuire, Routt Co., Colo.			(25)	
	Skinner, Yellowstone	$(1/8^x)$	$(1/4^x)$	(4)	(8)
Antelope	Skinner, Yellowstone	$(1/8^x)$	$(1/2^x)$	(16)	(39)
Buffalo	Skinner, Yellowstone	$(1/8^x)$	$(1/4^x)$	(8)	(22)
Mountain Sheep	Skinner, Yellowstone	$(1/16^x)$	$(1/4^x)$	(11)	(36)

^{x} Greater during migration.
* Artificially raised birds released at 8 weeks.

dard says the covey range during the fall or winter is often under 400 yards. The ranges overlap. The daily mobility in fall and winter must be under this. Every quail hunter who has followed tracks in snow, or reworked the same ground on successive days, knows that the daily radius in fall is often as low as 100 yards.

The foregoing paragraphs portray the known mobility of bobwhites. In all probability the quail is the least mobile species of American game. Table 5 attempts to portray, in addition to the few figures based on banding, the *estimated* mobility of the important non-migratory game species. All the figures in parentheses represent opinion. All that can be said for Table 5 is that it is better than nothing at all.

Predators are not included in the table. Most predators, even the non-migratory species, are more mobile than their prey. The extreme of mobile predators is probably the cougar, which has been actually tracked over hunting routes 100 miles in length and ranges 50 miles in diameter (E. S. Barker, unpublished).

The estimated mobility of some game mammals is given in Fig. 10.

Flight Limits. Somewhat allied to the property of mobility, but of lesser importance to game management, is the distance which various species of birds can or do traverse at a single flight. This is important only where it is intended to confine stocks of game on islands, or where the spread or interchange of individuals across rivers or other barriers is of consequence. Table 6 assembles the fragments of information available.

The accuracy of the figures on distances "successfully flown" varies from good to poor. As an example of the best accuracy, take the figure indicating that bobwhites in Clayton County, Iowa, flew one-half mile. Doctor J. F. Walter of McGregor, while fishing on the Mississippi River near St. Paul's Slough, has repeatedly seen a certain covey fly across the river at a certain point. For this section of the river, there happens to be a very accurate large-scale map, prepared by the Army Engineers for navigation improvements. The distance flown was scaled from this map, and is highly accurate. Apparently this same covey once tried this same flight in a fog, and was drowned, the bodies being picked out of the river by Doctor Walter.

The least accurate figures are based merely on recollection and estimate, but usually in surveyed farm territory where the observer knew the land lines or farm units.

The column on "flights not attempted" is based on islands of known distances from shore, and containing populations believed to be isolated.

The column on flights "unsuccessfully attempted" is based on observed drownings, or inference from drowned birds.

There is a doubt, however, whether drownings are always proof that the bird was physically incapable of negotiating the required distance. Thus Johnson (1819, p. 37) records the drowning of a covey of Hungarian partridges in the sea after a flight of only 300 yards from a cliff, whereas in other instances this species has been known to fly a mile. Johnson thinks the birds were "either intimidated or otherwise affected by that element" (the sea) rather than exhausted. I also know of cases where pheasants doubled back after a long flight over water. Such birds might be picked up drowned, or even be seen to drown, after negotiating a distance actually greater than that necessary to complete the flight originally intended.

Rate of Spread. Another property doubtless allied to the ordinary property of cruising radius, yet by no means wholly dependent on it, is the rate of spread into unoccupied range. Obviously this depends on how favorable the range is, and on the population pressure within the occupied zone, as well as on the freedom with which the species moves.

Pinnated grouse and whitetail deer in the Lake States spread north with settlement. The pinnated entered Wisconsin about 1840 and reached Lake Superior around 1920 or earlier, a spread of 300 miles in 60 years, or 5 miles per year (*Game Survey*, p. 164).

Spread in a native species, however, seldom has clean-cut points of beginning and ending, and invariably depends on the rate of change in the environment which is the cause of the spread. Hence it does not constitute a true measurement of the capacity for spread. Exotics planted at a single spot, in a large block of range already fit to receive them, afford a truer measure, provided the spread of the original plant be not masked by subsequent plantings at new spots.

Thus Hungarians spread from a plant in Ohio, probably at Defiance, to the north line of Lenawee County, Michigan (60 miles), between 1915 and 1928, a rate of nearly 5 miles per year. Yeatter (unpublished) in an independent calculation of this same species in the Michigan end of their movement between 1920 and 1927 arrived at a rate of 3.5 miles per year.

Hungarians spread 40 miles from Waukesha almost to Madison, Wisconsin, 1910–29, a rate of 2 miles per year. The plants at

Table 6

FLIGHT LIMITS

Species		Date	Distance, Miles: Successfully Flown	Not Attempted	Unsuccessfully Attempted
Bobwhite	Round Island, Miss.	1925		3	
	Alton, Ill.	Fall			*1/2 +
	Georgia	Winter	1/3		
	Jefferson Co., Ind.	Fall	*1		
	Clayton Co., Iowa	Sept.	x1/2		
Pinnated Grouse (Prairie Chicken)	Chambers Isl., Wisc.	April, 1927	7		
	Wisconsin	1930	12 to 15		
Ringneck Pheasant	Corvallis, Ore.	Oct. 1925	3		
	Sapeloe Isl., Ga.		#2		
	Okiboji Lake, Iowa	Spring	*1		
	Island in Clearwater Lake, Minn.	Nov. 1930	1/2		1-1/2
	Lake Pepin, Wisc.	Oct. 1931			3
Hungarian Partridge	Michigan		1/2		
Ringneck Pheasant	England		4		
Hungarian Partridge	England	Fall	1 (with the wind)		
Red Grouse	Britain	?	6 to 11		
Black Game	Britain	?	2		

*Flight started from a high place.
xDistance scaled from an accurate map.
#Also saw 4-5 mile flights in 3 stages.

the source were repeated almost yearly, thus inducing an artificial population pressure at that spot.

Lawton (1931) records the spread of Hungarians from Calgary, Alberta, where they were planted in 1908 and 1909, to eastern Saskatchewan by 1922. After 1922 the spread was masked by new plantings and cannot be used as a measure, although it now has proceeded east into Manitoba. Bradshaw (1922) states that the first bird reached Valor, Saskatchewan, by 1922, a distance of 400 miles from the original planting at Calgary in 1908. This is at the rate of 400 miles in 14 years, or 28 miles per year, —probably a record rate for a game bird.

South Dakota pheasants, while they spread rapidly, do not offer any reliable spread figures, since the first private plantings in Sphink County in 1908 were followed up by widespread plants in 1911 which masked the expansion of the original stock.

Even the most rapid instances of spread in a terrestrial game bird falls short of the maximum rates in more mobile passerine birds like the starling. This species, planted at New York City in 1890, reached Madison, Wisconsin, and bred there by 1928 (Cooke, 1928). The distance is 800 miles, the rate 21 miles per year. However, the last 700 miles of spread took place after 1914, a rate of 50 miles per year, or nearly twice that of the Hungarian partridge in the wheatlands of Canada.

While spread in the instances here cited is direct evidence of productivity, the game manager should remember that not every appearance of a new game bird is true spread. Drifting birds may appear as a result of dispersed plantings, or after eviction by fire, in which event they constitute evidence not of productivity, but of the opposite condition. Time will tell.

TOLERANCES

Environmental Tolerance. In the next chapter the number of environmental types included within the unit range of various species will be discussed. The species seem to differ in their tolerance of variation in the number, proportion and interspersion of these types.

For instance, under certain conditions in the Ozarks, and in the pine forests of the South, quail persist in small numbers on range consisting entirely of woodland, whereas normally a proper quail range includes at least five types, namely woodland, brush, weeds, grass, and cultivation. On the other hand, quail are known to persist in Kansas in the complete absence of woodland or brush. Quail, therefore, may be said to tolerate nearly 100 per cent variation in woodland and brush.

Antelope normally exist on 100 per cent prairie, but on the Gila and Coconino National Forests in New Mexico and Arizona they tolerate up to 50 or 75 per cent timber, consisting of open stands of yellow pine, or open juniper and pinyon.

Pinnated grouse normally inhabit range consisting entirely of cultivation and grassland, but in northern Wisconsin they tolerate a high percentage of timber and brush. Sharptail grouse, on the other hand, do not seem to tolerate the complete absence of timber or brush, at least not in the lake states. Grange (unpublished) points out that in the vicinity of agricultural settlements in northern Wisconsin there is a clear demarcation between the breeding zones of pinnated and sharptail grouse, the former surrounding the central and more cultivated areas near town, and the latter breeding in the peripheral zone of decreasing cultivation, including the outlying range composed entirely of brush, grass, and timber without cultivation.

Comparisons of range composition as between regions are of course a different matter from variations tolerated by a species within a single region. It seems likely that the tolerance of any species is greatest near the centre (presumably optimum) of its geographic distribution. Thus pinnated grouse in the region of Champaign, Illinois, persists in small numbers in spite of the complete demolition of original prairie, and the almost complete absence of grass or weed coverts, whereas in southwestern Wisconsin, under comparable devegetation, the species is fast disappearing.

All species now using grain and cultivated land of course originally tolerated the almost total absence of this type. Bogardus (1874) gives a convincing description of how the pinnated grouse in Illinois at first refused corn as either food or cover, but later learned to like it. They now, of course, largely depend on it as winter food in many localities, and on the Champaign prairies they depend on it as winter cover also.

Anderson (1907, p. 233) points out that the prairie chicken in Iowa, now nesting almost entirely in sloughs and marshes, originally chose the upland prairie hillsides. Lewis and Clarke found elk, deer, grizzly bear, and mountain sheep on the flat plains of Nebraska, a country very different from the mountain forests with which we now associate these species. A more recent instance is the upward altitudinal shift of the coyote in the West. The big game species first mentioned were, of course, forced upward by the pressure of human occupation, whereas the coyote probably followed the new food supply offered by range livestock. But it took him several decades to "learn" it was there, just as it took the prairie chicken a similar period to "learn" the utility of cornfields.

Many species, in short, display a tolerance of wide variation in the composition of their range. Sometimes this tolerance is acquired slowly by a process of adaptation; sometimes it seems to pre-exist as a kind of inherent elasticity or biological opportunism. For a given species tolerance is undoubtedly greatest where the intrinsic nature of the range is most favorable.

Tolerance Between Species. A question often discussed is whether pheasants displace bobwhite quail. Almost invariably such discussions proceed on the assumption that there either is or is not an innate antagonism between these two species. It seems much more likely that if such antagonism exists, it depends on the density of each species at the spot in question, quite as much as on any absolute specific relationship between them. In eastern Dane County, Wisconsin, there is an area nearly a township in size on which quail, ringneck pheasant, pinnated grouse, and Hungarian partridge exist together in an apparently stable and thrifty condition. The density of each, however, is thin. It seems likely that an increase in density of any of them would decrease the tolerance which apparently now exists. Such a decrease in tolerance would probably take place through competition for food alone.

Combativeness and the communication of disease are two other mechanisms affecting inter-species tolerance. It is becoming quite clear, for instance, that all gallinaceous game birds are more or less intolerant of domestic poultry, by reason of diseases communicated from the poultry to the game.

In England it is recognized that a dense population of Hungarian partridges will not tolerate more than a low density of pheasants on the same area (Maxwell, 1911, and Page, 1925).

In his pheasant book (1913) Maxwell cites one 5000-acre estate in England successfully carrying a breeding stock of 1000 partridges and 200 pheasants. Where heavier stocks of partridges are to be carried, he advises cleaning out the pheasants each fall, and renewing them artificially each summer. This implies that winter is the season of conflict. Food does not appear to be the sole reason for incompatibility, however, since Maxwell says that no amount of extra feeding can make it safe to overstock a partridge range with pheasants. He thinks that more head of killable game is secured in the long run where the two species range together. Whether he ascribes this to an only partial overlap in their food requirements, or to the lesser fluctuation of the pheasant crop, is not clear.

During the last low in the grouse cycle, there was much discussion of pheasants displacing pinnated grouse in South Dakota; likewise Taverner (1927) reported that Hungarians were displacing sharptail in the Canadian wheat belt. It is too early to judge the actuality of these apparent displacements. If the grouse fail to come back to normal during the next two or three "highs," there will then be grounds for believing that exotics are tending to displace them. During the present high (1932) they have come back, at least in some places.

Unexpected kinds of intolerance between species sometimes occur. Thus Stoddard reports turkeys eating quail eggs in Georgia. Errington reports a domestic hen killing a wild quail chick. I have second-hand reports of pheasants killing nestling cottontails, an adult quail, and an incubating prairie chicken; how often this happens is unknown. Management is concerned with trends and probabilities, not with possibilities or exceptions.

Density of Mixed Stands. When two or more allied species occur on the same range, what density limits hold for their combined numbers?

This interesting question is our best approach to the question of tolerance between species. It has, as already noted, been much written upon in Britain, but not in quantitative terms or census figures. The accurate quantitative work so far done in this country, such as Stoddard's and Wight's, has either applied to range inhabited by only one species, or to densities so low as to throw no light on the problem of mixtures.

In considering this matter, let the reader exclude from his mind those instances where two species are interspersed, but not mixed in the sense of occupying the same vegetative types. Thus pinnated and ruffed grouse are interspersed on many a tract in the Lake States, but they occupy the opens and thickets respectively, with only a small overlap at the peripheries of these two types. Such interspersions are not mixtures.

In glacial swamp country there are likewise frequent interspersions of pheasants with quail, pheasants with ruffed grouse, and ruffed grouse with quail. These represent intermediate degrees of true mixture.

A true mixture, often in heavy density, is found between pheasants and Hungarians in northwest Iowa, and between pheasants and quail in central Iowa. The Iowa Game Survey (1932) made a census of all game birds on some 500 farms during the winter of 1931–2, from which the following farms are selected as the densest mixtures of species:

The prairie chickens may be partially disregarded because they are migrants present in winter only, and the ruffed grouse as partially interspersed rather than mixed with quail. The other combinations, though, are true mixtures, and having been selected from hundreds of samples for high density, they are also presumably optima or near-optima for one or the other of the species in question.

The accuracy of the census figures is variable, but probably within 25 per cent in all cases. Winter concentrations of pheasants are excluded except in one figure (0.6 acres per bird for Linn County). On many of these farms from 50 to 100 pheasants had been killed before the census was made, but these removals may have been offset by subsequent influx and reshuffling.

The mixed densities in the last column seem to approach but seldom exceed a bird per acre, in the same manner as the densities for quail alone approach the same limit in this and other states. The table constitutes at least an indication that mixed stands are to a large degree subject to the same combined saturation point as would hold for pure stands of the constituent species.

From these data this rule-of-thumb may be tentatively laid down: Do not count on improving the total stand of upland game birds by adding new species requiring the same kind of range as the species already there. Building up what you already have will usually accomplish the same result at less risk and less cost.

TABLE 7

MIXED STANDS OF HIGH DENSITY

Maximum total game birds on Iowa farms, Iowa Game Survey, winter 1931–2

County	Acres in Farm	Census						Mixed Density Acres per bird
		Pheas.	Hun.	Quail	Ruffed Grouse	Prairie Chicken	Total	
Clayton	490	6		175	24		205	2.4
Dallas	120	25		75		4	104	1.9
Clay	160	81	8	12			101	1.6
Kossuth	160	100	12				112	1.4
Mills	1000	60		700			760	1.3
Jackson	218	15		150			165	1.3
Jasper	200	50		100		*1	151	1.3
Polk	300	150		100			250	1.2
Boone	160	30		100			130	1.2
Lyons	160	110	28				138	1.2
Davis	170	12		140			152	1.1
O'Brien	200	150	45				195	1.0
Sioux	160	80	10			*75	165	1.0
Washington	200	100		100			200	1.0
Palo Alto	200	175	80				255	0.8
Story	200	50		200			250	0.8
Linn	160	227		50			277	0.6

* Probably migrant winter visitants.

Minimum Units of Range and Population. Ordinarily a species cannot successfully inhabit a unit of range smaller than that required for the exercise of its daily cruising radius. Thus a 2-acre woodlot surrounded by cultivation will not hold ruffed grouse, whereas a 20-acre one may do so. It follows from this that the minimum unit range is high in the mobile species, and low in the non-mobile species. This principle of course bears strongly on the minimum unit on which game management can be successfully practiced.

In addition to the minimum geographic unit of range, there appears in some species to be a minimum population unit, or minimum density of population, below which the species fails to thrive. To account for this failure, the older writers on game conservation hypothecated a "point of resistance" or minimum population, below which the species, for reasons unknown, fails to respond to "protection."

The frequent failure of antelope to "come back," even under completely closed seasons, is a case in point. Such failures have been attributed to the species having fallen below its "point of resistance." The actual nature of the phenomenon may be accounted for under a theory advanced by A. G. Wallahan, a frontiersman and pioneer wild-life photographer of Routt County, Colorado. Wallahan observed that antelope herds of less than 12 or 15 individuals usually do not fight off wolves or coyotes *as a herd*, but when attacked by these animals will stampede and scatter so that weak individuals are readily cut out and run down, by relay or otherwise. Herds of more than 15, on the other hand, usually stand their ground as a unit, bunching into a defensive formation which enables the bucks to fight off the attacking wolves.

While this is simply a theory based on observation, it has the ring of probability, and may have many counterparts awaiting discovery and verification through research.

In a cyclic species like grouse it is easy to see how an epidemic, or a flight of goshawks, or a crusted snow, might make a clean sweep of a small unit of range such as an island, the isolation of which would prevent prompt restocking by influx from surrounding range. Possibly, therefore, the frequent absence of ruffed grouse from suitable islands, already described in Chapter III, is a phenomenon of minimum range units.

The simplest explanation of the minimum unit of population, and one which probably fits most actual cases, is the "clean sweep" which any local misfortune may make of any small detached colony of animals. Local and temporary exterminations occur on every game range. Where there is no surrounding population to restock by influx, the extermination is permanent. Low mobility of course decreases the probability of restocking; high mobility increases it. Thus mountain lions and wolves have been "exterminated" almost annually from many western regions, but as long as there are any left in neighboring regions, the blanks promptly restock. Iowa has experienced the restocking of many blank counties by prairie chickens during certain years of heavy winter influx of migrants from the North. Migrant chickens are, per se, of high mobility. On the other hand when a blizzard makes a clean sweep of non-mobile quail in one of the northern states, it has often required over a decade for natural restocking to take place. The same kind of loss in southern and more continuous quail range is often replaced in a couple of years.

Transplantation. No other property of game species has been explored with as much persistence, and with as little guidance from either science or experience, as that of susceptibility to transplantation. This term is here used to include both the introduction of exotics, and the planting of natives outside their natural range.

Transplantation of game is as old as civilization. Pheasants, for example, were introduced into Britain, possibly by the Romans, although they are not mentioned in English literature until 1059 (Leffingwell, 1928). They may not have been native to Europe at all, some believing they were brought there from Asia by the early Greeks.

An excellent summary of American experience in transplantation of game birds has been compiled by Doctor John C. Phillips (1928). One of his most valuable contributions is his classification of types of response by planted birds to their new environment. The following types of behavior in plants of game birds are taken from Phillips, except Types *D* and *F*, which have been added.

First of all, there are three types of failures:

(*A*) The planted stock immediately disperses and disappears without breeding. This may be called "*dispersal failure.*"

(*B*) The planted stock breeds for one or two years (often vigorously the first year) and then persists as non-breeding adults which gradually disappear. Sometimes there is no breeding, but simply the diminishing persistence of adults. This is a very prevalent type of failure, independently noted by Phillips and the Game Survey, and may be called "*straggling failure.*" Sometimes after vigorous breeding the first year, the entire stock suddenly disperses.

(*C*) The stock persists as a small breeding colony but does not spread. Usually it eventually disappears entirely. This may be called "*colony survival.*" From the viewpoint of producing a stock of shootable game, it is a type of failure. It inter-grades with straggling failure.

Secondly, there is a type of behavior representing partial success.

(*D*) The stock persists and sometimes spreads, but only with the aid of artificial propagation or the addition of new plants, or both. Because of the difficulty of distinguishing this type from the next, and in order to be perfectly just to pending projects, this type may be called "*artificial establishment.*" It is added to Phillips' classification because it may become important as a type of game management for pheasants in certain regions.

Thirdly, there are two types of success:

(*E*) The stock breeds and spreads (sometimes very vigorously at first) but experiences a subsequent partial decline to a lower level. This may be called "*recessive establishment.*" There is complete inter-gradation with Types *C* and *F*.

(*F*) The stock promptly and vigorously breeds and spreads, and shows complete *establishment* as a wild population. Plants which at first appear to be of this type may later exhibit recessive behavior and prove to be of Type *E*.

An incredible amount of misunderstanding, and a tragic waste of energy and funds, have resulted from the almost universal failure of sportsmen and game administrators to distinguish between establishment (in the sense of wild populations able to maintain themselves over a period of years) and the *B* and *C* types of failure or the *D* type of partial success.

It must here be said with all possible emphasis that success cannot be distinguished from failure on any given range until planting and artificial propagation have both ceased for at least three years. If, after three years, the stock still shows capacity to breed and spread, it may be called an establishment. If not, it must be regarded as a potential failure, and the further expenditure of funds or effort proceed with the same caution that ought to characterize putting good money after bad.

Most of this waste and confusion arises from the assumption that the property of transplantation is determined solely by the obvious or external characters of the environment. If the climate, food, and cover on the planted range superficially resemble that found in the bird's indigenous range, it is assumed that success is inevitable, provided only large enough plantings are made in the right way for a sufficient period of time. It is perfectly true that large and persistent plantings sometimes succeed where small or sporadic ones fail, but it is also highly probable that the successful transplantation of a species is often determined by factors as yet invisible and unknown to science, and therefore invisible and unknown to sportsmen.

Table 8 attempts a classification of the types of behavior shown by plants of various species in various parts of North America. Most of the historical information is taken from Phillips, from McAtee, and from the Game Survey, but the classification of behavior is the author's. Plantings less than three years old in 1930 are omitted.

The history of each plant is often meagre, and the intergradation between types of behavior complete. Many readers will take exception to the classification. However open to challenge it be as to detail, it shows conclusively that only two exotics have so far exhibited any large areas of successful establishment in this country, namely the ringneck pheasant and the Hungarian partridge. It is also clear that the only native species exhibiting any appreciable degree of success outside their natural range are the quails.

Every species that shows any success at all, shows almost all degrees of success in various regions, and what is still more to the point, it also shows almost all degrees of failure in other regions.

Table 8 shows no single instance of the successful transplantation of a cyclic species outside its natural range in America. In Europe, however, the cyclic red grouse of the British Isles has been successfully transplanted to two or three small ranges in Sweden and Belgium.

Fig. 8[1] pictures the geographic distribution of success and

[1] *Explanation of Fig. 8. Accuracy.* West of the Missouri River the map is very rough, due to the great difficulty in getting comparable information from the various states, and the complexities introduced by altitudinal zones.

Source of Data: R. E. Yeatter of the University of Michigan (who will publish more detailed maps later), John C. Phillips (1928), McAtee (1929), and the Game Surveys.

Symbols. Two large circles mean two successive attempts at statewide plantings. A

TABLE 8

SUCCESS OF GAME BIRD TRANSPLANTATION

Tabulated from "Wild Birds Introduced or Transplanted in North America" - by John C. Phillips, "Game Birds Suitable for Naturalizing in U.S." - by W.L.McAtee, and "Game Survey" - by Aldo Leopold

Species	Failure		(c) Colony Survival			
	(a) Dispersal (Disappeared without breeding)	(b) Straggling (Bred at first but gradually disappeared)	(Survived but did not spread)	(d) Partial (with aid of artificial restocking)	(e) Recessive	(f) Complete
EXOTICS INTRODUCED						
Ringneck Pheasant (various mixtures of races) (See Fig. 8)	Instance: Mo.(Game Survey, p.109,111)	Instance: Ind.(Game Survey, p.110)	Instance: Mo.(Game Survey, p.112)	Sapeloe Isl., Ga.	Willamette Valley said to have shown recession	See Fig. 8
Reeves Pheasant	—	Wash., N. J.	—	—	—	—
Golden Pheasant	Calif.,Wash.,B.C., Va.	Ill.,Fayette Co.,Ind.,B.C.	—	—	—	—
Silver Pheasant	—		—	—	—	—
Hungarian Partridge (See Fig. 8)	Instance: S. Ill., Ind. (Game Survey, p.110)	Instance: See Phillips p. 34, Game Survey, p. 111	S. Me., Cent. Conn., N. Mo.(Game Survey,p.112), N.E.N.Y., E. Pa.	Possible instance: S.E. Minn. (Game Survey, p.113)	Parts of Washington said to have shown recession	See Fig. 8
Guinea Fowl	—	Jekyl Isl., Ga., Cal.	—	—	—	—
Black Grouse	Grand Isl.,Mich., B.C., Me., Ont.	Newfoundland, N. Y.	—	—	—	—
Capercailzie	Me., N.Y.,Newfoundland, B.C.	Grand Isl., Mich., Ont.	—	—	—	—
Red Legged Partridge	Ill.	—	—	—	—	—
Egyptian Migratory Quail	Quebec,Ont., Me., N.H., Mass., N.Y., N.J., Pa., Va., Ohio	Vermont	—	—	—	—
Migratory Chinese Quail	Wash., Calif.	—	—	—	—	—
Asiatic Sand Grouse	Wash., Ore.	—	—	—	—	—
NATIVES TRANSPLANTED OUTSIDE THEIR NATURAL RANGE						
Wild Turkey	Calif., Ore., Wash.	—	N. W. Ariz.	—	—	—
Pinnated Grouse	Calif., Wash., Mass.	Md., Me., Vt., N. Y., Mass., N. J., Pa.	—	—	—	—
Sharptail Grouse	Md., Conn., Mass., Vt., Grand Isl., Mich.	—	—	—	—	—
Scaled Quail	S. Cent. Wash., S. Cent. Ga.	La., Fla.	—	—	—	W. Kan.?, S.E.Colo.?
California Quail	N. Y.	Md., Del., Ill., Mo., Mass.	—	—	—	Parts of Nev., Idaho, Ore., Utah, Wash.?, B.C.
Gambel Quail	Pa., Ky., Okla., E. Colo., N. Cal.	Mass., Wash.	N. N.Mex., N.E. Ariz., San Clemente Isl.,Calif	—	—	W. Colo.
Mountain Quail	Mass., Ala., Neb., N.C.?, Mont.	—	S.W. B.C., Vancouver	—	—	Wash.?, W. Idaho?
Bobwhite	Nova Scotia, S. Dak., Manitoba	Calif., N.Colo., B.C.	E. N.Mex., W.Cent. Colo.	—	Utah, Idaho (see Phillips, p.29)	Parts of Wash., Ore., Idaho, E.Colo., W.Mont.

failure with pheasants and Hungarians up to 1930. It is a rough and generalized version of a detailed map being compiled by R. E. Yeatter for later publication. The map suggests these tentative conclusions:

(1) The Hungarian is much more exacting in its range requirements than the pheasant.
(2) Both species consistently fail in the south half of the United States (with possible exceptions in the mountain regions), and in forested regions.
(3) The spotty distribution of success, especially of Hungarians, in spite of almost universal plantings, suggests that success is determined by some environmental factor other than the more obvious aspects of climate, food, cover, or enemies.

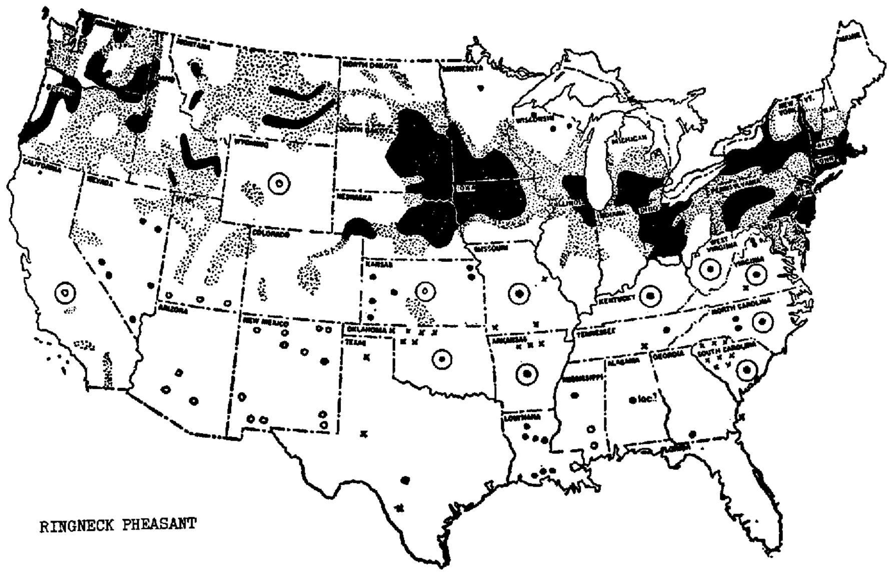
All of the foregoing discussion deals with birds. In game mammals, attempts at transplantation have taken place on a much smaller scale, partly by reason of the fact that many of our important game mammals have a transcontinental range, and partly because the human psychology which lies behind the impulse to plant strange species is somehow strongest in the case of birds. As a consequence little is known, or need here be discussed, concerning the transplantation of game mammals. Most of the rodents seem to transplant readily. There has been, for instance, a wholesale planting of western races of rabbits in the eastern states. The jackrabbit range has been extended eastward by plantings. European hares are spreading in southern Ontario, where they constitute a pest. American gray squirrels are a pest in England, where they have developed a cycle. Most ordinary American horned game except mountain sheep and antelope seem to stand transplanting easily.

The only predator known to have been transplanted in America is the red fox, which was moved to Texas by fox hunters in

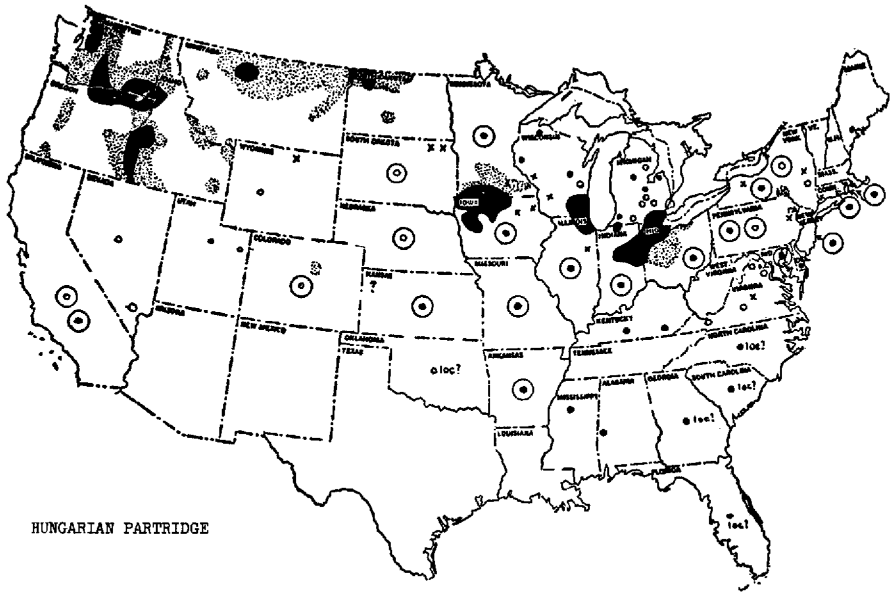
small solid dot followed by "loc?" means that the literature records failed plantings but does not specify their location.

The stippled areas include diverse categories which could not be differentiated due to the small scale of the map or due to lack of first-hand information. In the north central states stippling accurately shows thinly populated (or, in Wisconsin, incompletely planted) range. In the western states stippling includes mainly spotty distribution due to altitude and irrigation. In the eastern states stippling includes thin and spotty range and also (as in Maryland pheasants) range of indeterminate status as to establishment.

FIG. 8



RINGNECK PHEASANT



HUNGARIAN PARTRIDGE

LEGEND

Established Range, 1930		Plantings Statewide	Plantings Local	Result
▬	Good population established	⊙	•	Failed, except as noted
▒	Thin, scattered, spotty, or doubtful	◎	o	Indeterminate, or too recent to judge success
x	Isolated colony			

Outline map, courtesy of Rand McNall

1891, and has become established there in several counties (Texas Conservation Yearbook, 1929–30).

Domestication. The susceptibility of game species to domestication or rearing in captivity is a property which parallels that of transplantation. Naturally the species which can be reared in captivity are the most available for transplantation.

As in transplantation, there are various degrees of success. Table 9 classifies the maximum degree of success which appears to be characteristic of various species and groups. The information in the table is taken from Job (1923), and Hopkinson (1926). Experts can of course occasionally do better, and new discoveries may alter the results at any time.

The hatching or rearing of wild eggs is not credited as successful breeding in the table. The table indicates that, by and large, marine, migratory, and cyclic species cannot be reared in captivity, or if so, only with great difficulty. Most of the shore birds do not seem to survive in captivity at all. Many of the species successfully reared in captivity are those susceptible of transplantation.

There is of course nothing final about this classification. The technique of game farming is constantly improving and each year sees some heretofore insurmountable difficulty partially or wholly overcome. It is important to keep in mind, however, that efforts at domestication are often conducted regardless of the expense or trouble which they entail. That a species has been reared in captivity does not of itself constitute evidence that it can be reared on a scale and at a cost practicable for game management purposes. So far game farming, from the viewpoint of management, is practicable only for ringneck pheasant, most quails, wild turkey, mallard, and Canada goose.

All antlered game except moose can be bred in confinement (see Lantz, 1916). Other big game mammals are more difficult.

Cottontails can possibly be bred in semi-confinement (Hiller, 1932), but I know of no case in which close confinement has been successful. Dice (1929) records three litters bred and born in cages, but all of them were of the southwestern subspecies. Fighting between the male and female caused failure of all attempts to breed the eastern cottontail.

Susceptibility to artificial rearing is of importance to game management mainly as a source of seed for restocking ranges on which the species in question is exterminated, or for planting new or restocking shot-out range. It happens, however, to be a property easily dramatized to and visualized by the lay mind, and hence has received such a large share of public attention as to become, to the rank and file, almost synonymous with conservation.

TABLE 9

CLASSIFICATION OF AMERICAN GAME BIRDS AS TO DOMESTICATION

MAXIMUM DEGREE OF SUCCESS TO DATE	EXAMPLES
Not so far captive	Shorebirds Rails, except Coot
In captivity, but no eggs	Woodcock Coot Brants
In captivity, but infertile eggs	Cranes (except Little Brown) Sea Ducks (except species below)
Fertile eggs, but young die when partly grown	All Grouse, with rare exceptions in Ruffed Grouse and Prairie Chicken
Successfully bred in captivity. (Hatching or rearing of wild eggs not credited as success.)	Hungarian Partridge Pheasants All Quails Turkeys River Ducks, also Redhead, Canvasback, Scaup, Golden-eye Swans Mourning Dove Passenger Pigeon Bandtail Pigeon All Geese (except Brants) Whitewing Dove Little Brown Crane (once)

A review of game farming technique will be given in Chapter XV.

SEX HABITS

Sex Properties. Each species of game has eight fundamental sex properties affecting management:

1. The age of sex maturity, or minimum breeding age.
2. The number of females served by one male.

3. Period of gestation.
4. The number of young per brood or litter.
5. The number of broods or litters per year.
6. The initial sex ratio in the young at birth.
7. Maximum breeding age.
8. Longevity beyond maximum breeding age.

Each of these properties is known to vary more or less with environment, but these variations within the species are usually distinctly smaller than those between species. In a "perfect" environment these properties would give rise to a population of fixed composition as to sex and age for each species.

In all actual environments, however, there are radical departures from this theoretical norm. The measurement and comparison of these departures is one of the principal means for the diagnosis of field conditions, and their beneficial manipulation one of the principal activities of management.

Numbers 1, 4–5, 7, and 8 have already been discussed in Chapter II for the purpose of deriving the breeding potentials of the various species.

There remain to be discussed to what extent these characters constitute properties of various groups, and what important disturbances of the normal condition are likely to be encountered or used in game management.

Lack of Information. The paucity of our information on these properties is indicated by the fact that of the 36 species of birds in Table 1, the literature indicates conclusively in the case of only 9 at what age they first breed, in the case of only 9 whether more than one brood is raised per year, and in the case of only 8 what type of mating is characteristic.

The mammals are in somewhat better case.

It is, of course, difficult to establish these characters underlying reproduction, especially in species not subject to domestication, or not easily trapped for banding, or in species in which sex and age are not distinguishable in the field. Nevertheless they are of such fundamental import to both science and conservation that it seems fair to suggest that our professional naturalists should give them more attention. The minute study of the bones and the pelage of dead specimens can, to be sure, teach us much of the evolutionary processes by which the species came into being, but hardly more than the study of the means by which it still holds its place in the sun. The latter may, moreover, point out ways in which that place can be retained, whereas the former cannot.

The following captions give as good an account of breeding characters as the existing paucity of information permits.

Breeding Age. Poultrymen say that in domesticated birds minimum breeding age sometimes differs as between sexes. Whether the stock was hatched late or early also doubtless affects the probability of one-year breeding.

Thus wild geese in confinement quite certainly do not breed until two years old. There is no record of eggs from yearling females, although yearling males may possibly mate (Halpin, unpublished). In tame varieties, ganders sometimes have the capacity to breed at one year, though females have neither the capacity nor the inclination (Halpin).

In domestic turkey, yearlings of both sexes are preferred as breeders. Hens over three years are rejected (Jull and Lee, 1928).

Wild turkeys, however, do not breed as yearlings. Wild gobblers in confinement first breed at two years (Quarles, 1918), although yearling hens have been known to breed and rear young (Enty, 1897).

In the case of turkeys, domestication has evidently advanced minimum breeding age, both as to capacity and inclination.

One may possibly infer from these authorities that in waterfowl the male matures first, and in upland game the female. It is also reasonable to suppose that in wild polygamous birds the young male may not be allowed to breed as early as he is physically able to do so.

With this background, we are now ready to consider the minimum breeding ages characteristic of wild game species, already outlined briefly in Tables 1*a* and 1*b*.

It is probable that all American upland game birds except wild turkeys breed as yearlings. The probabilities are that wild turkeys actually breed at two years.

In waterfowl, it is certain that wild geese do not breed until two, and swans until three or more years old. I suspect that cranes may not breed until two or more years old. In ducks and shore birds, it is by no means certain that all of the species breed as yearlings. Mallards undoubtedly do. Works on artificial propagation of ducks seem to assume that they all do, but they likewise mention how hard it is to get fertile eggs in many species. In Wilson snipe and woodcock we lack the analogy of captives. Non-breeders are plentiful in many species of shorebirds. It is not at all impossible that many waterfowl defer breeding until the second year.

This lack of fundamental information about ducks and shorebirds is a regrettable hiatus in our ornithology.

It seems quite certain that all the smaller game mammals breed at one year. Some have suspected the cottontail of breeding sooner, but a May rabbit, even if mature at six months, could hardly have young before November. Young are not seen at that season, and could hardly survive. Domestic "rabbits" are bred at five or six months of age, but these are actually hares, and are not a sound analogy.

None of the big-game mammals bear young at less than two years. Some big-game species, such as elk, sheep, buffalo, and bears reach maturity only after three or four years. This character of deferred breeding is of great importance, as will be evident by a study of the breeding potential curves in Fig. 3. A species with the breeding index 1–2 (breeding at one year, two young per year) reproduces only a little slower than one with the formula 2–6 (breeding at two years, but with three times as many young per year). Broadly speaking, the litters or broods must be more than doubled to compensate for 2-year instead of 1-year maturity.

Maximum breeding age is almost totally unknown. Coleman (Stoddard, p. 455) observed a high egg record in a captive bobwhite hen up to at least the sixth year.

Barren individuals, if there are such, use up range and food without contributing to productivity. Declining reproductive vigor may affect productivity, even without barrenness. The British, for instance, are persuaded that their success in grouse management is largely due to the automatic reduction of old birds effected in driving, and the deliberate killing off of old cocks by the game keepers (Leopold and Ball, 1931*a*). When the driven grouse come over the guns, the old birds come as singles or pairs and are usually killed, while the young come over in packs or flocks, and thus suffer a lesser per cent of mortality.

That driving effects a differential mortality among young and old may be considered an established fact. Whether old birds are markedly inferior as breeders should be pondered with more caution. It seems probable, but is not proved. *The Grouse Report*, a scientific publication, accepts the theory and explains its workings as follows:

(1) Old cocks appropriate a larger breeding territory than young ones, and thus reduce the number of breeding pairs which can be accommodated on a given acreage.

(2) Old parents produce smaller clutches with a lesser percentage of fertility than young ones.

The first point sounds highly probable. The second seems entirely possible. Neither, however, is as yet supported by quantitative evidence. Both offer an entrancing field for research.

McLean (1930*a*, p. 19) suspects that superannuated California quail form separate coveys which inhabit high ridges apart from the range of younger birds, and which do not pair or nest, even in good years. He cites numerous examples, including a flock of 80 of which he took specimens.

> "Upon dissection . . . I came to the conclusion that they were very old, and sexually spent. Their bones were brittle, legs rough and scaly, and the sexual organs diminutive in both males and females. Other birds do not seem to mix with them, even in winter."

Young Per Year; Second Broods vs. Renestings. The average size of clutches or litters, as shown in Table 1, is quite well established for all game species, but the number of clutches or litters per year much less so, especially in birds.

The only game bird known to raise regularly two or more broods yearly is the mourning dove. Barrows (1912) suspects the passenger pigeon did, and the bandtail pigeon may also.

The ringneck pheasant and the California quail *sometimes* raise two broods. Wight (1930, p. 224) says of the pheasant in Michigan, "Early nesting females usually again build nests and rear a brood," but he is referring to renestings following destruction of the earlier nest, not a second brood following the rearing of an earlier one. Beebe (1922) says that the ringneck in its native Asiatic range "sometimes breeds twice," but no equivalent assertion is made for the other component of our American hybrid, *P. colchicus*.

McLean (1930*a*) cites a one-legged California quail hen seen to raise two broods for two years out of three. It is extremely doubtful, however, whether two broods are sufficiently common in any gallinaceous bird to affect the breeding potential. Stoddard is quite certain that second broods do not occur at all in bobwhite.

Both sportsmen and naturalists might be less credulous of stories about second broods if they stopped to add up the time liabilities involved. These may be roughly computed for almost any gallinaceous bird to be:

DAYS	ITEM	CALCULATION
20	Laying a clutch	14 eggs at 1½ days per egg
2	Interval	
23	Incubation	
40	Dependency of young	Usually at least 6 weeks
85		

A hen starting her first clutch on May 1 could therefore not rear that brood and be ready to start a second before the elapse of 85 days, which means July 25. A new nest started July 25 would hatch September 10 and would not be independent until October 20.

That the California quail is the only American game bird in which second broods occur with sufficient frequency to affect productivity gains further probability from the extraordinary length of the summer season on its range. The same reasoning applies to the other Southwestern quails, but is so far not supported by affirmative observations.

The improbability that second broods are frequent in pheasant is further attested by Wight's observation that the cock starts to moult, and becomes solitary, before the first brood is old enough to leave the hen.

Second broods should be sharply distinguished from renestings.

Many game birds, of course, renest one or more times *if the preceding nest is destroyed.* Some, like the quails, persist in their attempts until the weather becomes unsuitable in September. Such attempts following earlier failures are called re-nestings.

Apparently if the nest destruction takes place before hatching, the nesting instinct continues operative; if after hatching it becomes inoperative for the remainder of the year. The exact line of demarcation is not positively known. It may vary with circumstance and species. Some species may not renest at all.

It is a curious fact that the popular supposition, so prevalent in America, that quails or other gallinaceous birds raise two successive broods, should never have taken root in Europe. It arises, of course, from seeing small young in fall—which are actually the product of renesting following earlier nest mortality, and the shifting of young between coveys.

One popular supposition is that the cock bird takes over the *care* of the first brood while the hen lays another clutch. Leffingwell (1928) mentions that this may possibly occur in pheasants. He once observed a cock leading a brood. Wight's observations on the moult, however, render this unlikely.

An interesting variation of this is Sprake's theory (1930) that the English partridge may sometimes lay two clutches, the first of which is incubated by the cock, and the second by the hen. Neither of these suppositions has ever been verified.

In the game rodents (rabbits, hares, and squirrels) the number of litters per year is virtually unknown. The breeding potential curves in Fig. 3, although based on correct size of litters, are, for lack of data on litters per year, nothing but a conservative guess.

In bears we have the unique probability, suggested by Wright and Seton, that females bring forth only in alternate years. This of course makes the young per year only half the average litter. Luttringer (1931) suggests that elk cows breed only every four years, but in the absence of confirmation by other authorities Table 1*b* assumes yearly breeding.

In antlered game it seems fairly clear that a young doe is less likely to twin at her first bearing than at subsequent ones. The long gestation of course precludes more than one birth per year. The lesser productivity of young females in antlered game is a reversal of the British supposition that in gallinaceous birds, young females lay larger clutches of higher fertility than old ones.

In domestic mammals, the average fecundity of an individual female gradually rises, as in deer, to an age of optimum fecundity, and then gradually declines. In domestic fowls it rises sharply to an early optimum, often in the second year, and then gradually declines.

Mating Habits. The conventional categories of mating habits include monogamy, polygamy, polyandry, and promiscuity. Seton (1929), however, rightly feels the need of closer definition. He says:

"There are four degrees of monogamy among animals:

"1st. That in which a male and a female remain together for perhaps a week; after which the female no longer desires a mate, and the male seeks a second. That is, one mate at a time, but perhaps five or six in the season.

"2nd. That of certain weasels, wherein the pair continue together during the mating season of a week or more, then separate completely.

"3rd. That of hawks, in which the pair continue together with little interruption, until the young are able to care for themselves (say for four or five months), the father faithfully helping in caring for the young.

"4th. That of eagles, which pair and live together continuously, till one is removed by death."

Seton's categories may well be adopted as four standard subtypes of monogamy. Polygamy, polyandry (if it exists in game), and promiscuity may also need further subdivision, but the information for doing so is not at hand.

The distribution of mating types among the various groups of game species is a subject on parts of which we can make positive assertions, but as to other parts we must tread with caution until we know more about life history of game species.

Bobwhite in the wild, for instance, certainly practice monogamy of Seton's Type 3, *i. e.*, the pair breeds and continues as a pair until the young are grown, but not longer. Either the hen or the cock may incubate and rear the young. Alternation is rare. The circumstances determining which sex undertakes incubation eluded even so keen an observer as Stoddard.

Despite this well-established monogamous character in the wild bobwhite, Coleman (Stoddard, p. 458) freely induced polygamy in captive bobwhite by confining 12 hens with 4 cocks in "community" breeding pens. This indicates that mating characters may not be especially deep-seated.

Probably the other quails are similar to bobwhite.

All pheasants are certainly polygamous, but Beebe (1922) thinks that *colchicus* is less so than *torquatus*, the harems running

2–3 hens and 4–8 hens respectively. The black-necked *colchicus*, Beebe thinks, is sometimes monogamous. Since pheasant cocks are only rarely known to incubate, it may be assumed that this occasional monogamy, if it exists at all, is of Seton's Type 2. It seems more likely, though, that the apparent monogamy reported by Beebe is better explained by Wight's (1930) territorial type of polygamy. Wight has concluded that our hybrid pheasant in Michigan seldom shows harems of more than two or three hens, and that "harem" is really not truly descriptive, in that each female appropriates a territory, in which she nests. She does not join a community of females to be herded around as a "captive" group by their master. The group of nesting territories constitutes the "crowing ground" of the cock. He defends it against other cocks, but Wight thinks his interest is in the hen, rather than in the territory. This kind of mating may be tentatively designated as Wight's "crowing ground" or "hen-territory" type of polygamy. It may be found to prevail elsewhere.

The Hungarian or gray partridge, like bobwhite, clearly falls into Seton's Type 3 of monogamy. Sprake observed one case in which he thinks a single wild male apparently had two hens, each with a nest. Bracher (1931), however, cites some experiments at the Pilot Rock Farm in Oregon which indicate very strongly not only that Type 3 monogamy prevails, but that Type 4 does *not* prevail, nor does any degree of polygamy.

The various grouse present a perplexing problem. In spite of a large volume of descriptive literature on mating antics, we really know very little about the type of mating. We know that the red grouse of Britain is not only monogamous, but practices the same high type of monogamy as bobwhite (Type 3). The *Grouse Report* (p. 13) says: "They (the young) are anxiously guarded by the parents, the hen being more attached to them than the cock, who, when they are disturbed, is the first to fly from danger, though it may be only for a short distance. The hen, on the other hand, will risk any danger rather than leave her brood."

Contrast with this the probably promiscuous mating of the ruffed grouse and the pinnated, in which the male takes no part in the care of the young, nor is the existence of pairs an established fact. To be sure, each of the three species is of a separate genus, but all belong to the same family. Apparently a type of mating established for one species cannot be assumed to extend beyond the genus.

It would take pages to review what we do not know about mating types in American grouse. My interpretation of the somewhat conflicting evidence is that the ruffed grouse practices polygamy of Wight's "crowing ground" type, with these differences: the cock's "crowing" is mechanical (drumming) instead of vocal; the cock's location is fixed at a central series of drumming logs. The hens occupy nesting territories around the drumming logs, as in pheasants.

The mating of pinnated and sharptail is similar, except that several cocks (up to 30) collectively use a common dancing or booming ground, which is visited by the hens having territories nearby, instead of the cock visiting the hens, as in pheasant. The probable result is promiscuity, and these species are so classified in Table 1. Schmidt (unpublished) finds that the same knoll is used as a dancing ground from year to year, and in one case was not deserted even when plowed up. The nests are peripheral to and usually within a half-mile of the dancing ground.

As to mating types in our other grouse, no one seems to know.

Turkeys, according to Quarles (1918), practice polygamy of the true harem type, 4–5 hens being appropriated and herded about by the male until nesting time, when the hens nest nearby. In captivity, if there is only one gobbler present, he rejoins the hen as soon as the brood hatches, but if there is more than one gobbler, they all flock together until the broods are two-thirds grown.

Geese are certainly monogamous. The Canada goose follows Seton's Type 4 (lifelong) monogamy (Miner, 1923). The mating of wild ducks is still an enigma. Job (1923) says "ducks in wild state are normally monogamous . . . but tend to become polygamous in captivity." Grinnell (1918) says of the mallard, "this duck is monogamous in its native estate, although some authorities contend that polygamy occurs where there is a dearth of males." It seems likely that monogamy is normal for all the ducks when the sexes are balanced. Where unbalanced, the excess is likely to be of males (Lincoln, 1932). Promiscuity, or even polyandry, might be looked for under such conditions. The seemingly promiscuous mating of domesticated varieties supports the former assumption.

The game rodents are apparently all promiscuous except the fox squirrel, which Seton thinks may be monogamous.

Antlered game is probably all polygamous, with the possible exception of the moose and mountain goat. Seton says that the Scandinavian moose is considered monogamous, but concludes that our moose is evidently not. The whitetail, he thinks, is less polygamous than the other deer.

The bears follow Seton's Type 1 of monogamy.

An exact mental picture of the type of mating is often of great practical value to the game manager, especially in the manipulation of the sex ratio through hunting, and in the control of nesting cover. The finest of nesting cover would hold no chickens if too far from a dancing or booming ground. The finest of ranges may be only half productive if the sex ratio fails to fit the type of mating inherent in the species.

Sex Ratios. Geneticists believe that in any large sample of animal population the two sexes are originally conceived in equal numbers.

At birth, however, the original parity of the sexes has been more or less changed by pre-natal mortality. The direction and degree of these changes show more or less constant differences as between species or groups of species.

This characteristic sex-ratio at birth is unknown for any game species. To determine it requires laborious expert dissection of many newly born individuals, and this has not yet been done.

Certain domesticated animals, however, probably reflect the characteristics of their wild relatives. Table 10 gives figures taken from accepted authorities. These have been rounded off to whole numbers and converted to the per cent basis later used in the discussion of this subject.

TABLE 10

SEX RATIOS AT BIRTH

SPECIES	MALE : FEMALE RATIO	AUTHORITY
Man	51 : 49 to 52 : 48	Crew, 1925, p. 255
Horse	49 : 51	"
Dog	54 : 46	"
Cattle	52 : 48	"
Sheep	49 : 51	"
Pig	53 : 47	"
Rabbit	51 : 49	"
Fowl	48 : 52	"
Pigeon	51 : 49	Cole and Kirkpatrick, 1915, p. 465
Mallard	51 : 49	Jaap (unpubl.)

The sex ratio at birth is known to vary with the species, with race breed or strain, with the season of the year, and in different matings. It is radically disturbed in hybrids. It has been alleged to vary with many other conditions. Of the variations accepted as conclusive by geneticists, there are two of special import to game management.

Crew (1925, p. 258) says: "In the experience of many poultry breeders, the first lot of eggs laid by a pullet yields a preponderance of male chickens, whereas as the season advances and the pullet ages, the proportion of males steadily decreases." Friedman (1931) makes a similar assertion. More recent work, however, leaves this in doubt.

Again Crew (p. 261): "In the case of the (domestic) rabbit it has been shown that the sex ratio is related to the chronological order of the service of the buck; in the first service group there is a preponderance of males, and then an increasing preponderance of females."

This boils down to a probability that gallinaceous birds at birth will average a slight preponderance of females, but early eggs may show a male and late eggs an accentuated female trend. In ducks, there is some indication of an average trend to males.

The sex ratio at any time after birth is likely to be different from that at birth, by reason of differential mortality from disease, predators, or other factors. Such post-natal differences in mortality as between sexes may accumulate and reach large proportions. The degree of accumulation varies with the ratio of old to young in the population.

The differing mating habits of various species discussed in the preceding captions necessarily imply a different optimum of sex and age composition for each. A polygamous species like pheasant or deer can tolerate, or may even be benefited by, an excess of females, but it must not be too great. On the other hand, a monogamous species like bobwhite probably needs to retain the original close balance of the sexes; productivity might be seriously affected by a large disturbance of the ratio in either direction.

Management, theoretically, should frequently compare the existing ratio with the optimum, and regulate the system of shooting so as to bend the existing ratio toward the optimum.

This process should begin with a knowledge of what the optimum is, and how much disturbance it will tolerate. Such knowledge seldom exists, except as based on captives, and such evidence is not dependable. Thus Coleman, as already stated, induced polygamy in captive quail by an artificial shortage of cocks, but it is extremely doubtful whether a shortage of cocks in the wild could maintain productivity by polygamy. McAtee (1929*a*) advises 5–7 hens per cock for captive pheasants, but this ratio in a wild population would almost certainly be too low on cocks.

The only guidance as yet available for the American game manager consists of a very few rough measurements of sex ratios which *seem to be associated with* satisfactory or unsatisfactory productivity in wild populations.

Bobwhite Sex Ratios. The most authoritative of these measurements is Stoddard's on Georgia quail. In 20,000 bagged quail he found a winter average over a 5-year period of 53 cocks: 47 hens. The yearly averages varied from 52:48 in the medium or fair year 1925–6 to 55:45 in the poor year 1928–9. He also found that the same locality sampled at successive dates through the winter showed a small progressive decline in proportion of hens. He found that trapping consistently showed more cocks than the bags did in the same locality. The average difference was 2 per cent more cocks in trapping than in shooting. The shooting usually *preceded* the trapping. Stoddard seems to lean toward ascribing this difference between the two to the same progressive differential mortality in hens already noted. The same differential would explain the higher proportion of cocks in poor years, because in such years a higher percentage of the crop consists of old birds among which the differential has been working for a longer time.

Table 11 summarizes Stoddard's bag tally, and several others secured by him from other sportsmen in the southern states.

The Game Survey compiled a sex tally of 4184 bobwhites bagged by 25 sportsmen during 1929, 1930, and 1931, in as many localities in four states. The tally, summarized by states, appears as Table 12.

The average ratio falls within a half of 1 per cent of being identical with Stoddard's average of 53:47.

The season of 1929 was favorable; 1930 was adverse except in Minnesota (Leopold and Ball, 1931); 1931 was normal or above. The table indicates that the percentage of males was heavier during the adverse year 1930 than in the good year 1929, but the

TABLE 11

BAG TALLY OF SEX RATIO IN BOBWHITE
SOUTHERN STATES

Data by	Locality	Period	No. of Birds	Ratio	
				Male	Female
H. L. Stoddard	Georgia	1924–29	20,000	53	47
E. R. Coleman	Carolinas, Fla., Pa., Ala.	1894–1921	10,700	54	46
A. W. Elting	S.Carolina	1925–29	845	57	43
C. E. Buckle	Tennessee	1905–26	?	53	47

same as in the good year 1931. The three-year average for these four states is ½ per cent lower on cocks than Stoddard's five-year average for south Georgia. This fits in with Stoddard's theory of a progressive differential against hens, since midwestern quail are shot in November, whereas most Georgia quail are shot in January and February.

TABLE 12

BAG TALLY OF SEX RATIO IN BOBWHITE
NORTH CENTRAL STATES

State	1929				1930				1931				Total			
	Birds		Per Cent		Birds		Per Cent		Birds		Per Cent		Birds		Per Cent	
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F
Illinois	420	405	51	49	161	187	46	54	173	201	46	54	754	793	49	51
Indiana	190	182	51	49	258	193	57	43	168	108	61	39	618	483	56	44
Minnesota	17	20	X	X	45	35	X	X	60	39	X	X	122	94	57	43
Missouri					231	204	53	47	318	280	53	47	704	616	53	47
Totals	629	607	51	49	695	619	53	47	719	628	53	47	2198	1986	52.5	47.5

Seth Gordon (unpublished) superintended the shipment of 6,000 trapped Mexican bobwhites, in pairs, from Mexico in 1916. There were 800 cocks left over after the car of 3000 pairs had been made up. This indicates a total of 3800 cocks to 3000 hens, or a ratio of 56:44.

Gorsuch (1932) found a cock : hen ratio of 49:51 in 160 gambel quail trapped in three localities in Arizona during the winter of 1931–32. The number of birds is of course too small to be conclusive.

In general, it may be tentatively concluded that a 2 or 3 per cent excess of males is normal *for large numbers of bobwhites bagged in diverse localities.* Any greater excess should be regarded as a symptom of something wrong.

One man's bag made in a single locality during a single year may, however, depart widely from the norm. In the data on which Table 12 is based, the ratio for individual sportsmen bagging 50 or more birds ran as high as 67:33 and as low as 35:65. Smaller bags may of course show almost any ratio as a result of chance alone.

A heavier than normal percentage of males may possibly be expected on the edge of the quail range. The Minnesota average of 57:43, and the Mexican figure of 56:44 both tend to confirm this supposition. Conversely it may be significant that the only state showing an excess of hens is Illinois (49:51), which Fig. 6 assumes to be within the optimum range, or qualitative centre of geographic distribution, for the species.

Pheasant Sex Ratios. State Game Wardens Oscar Johnson of South Dakota (*Game Survey*, p. 118) and W. E. Albert of Iowa "shined" large numbers of wild pheasants for transfer to unstocked districts. This work was done during winter, after the open season had operated differently on the sexes. State Game Warden Burnie Maurek conducted similar operations in southern North Dakota, where no open season has as yet been allowed. No official records of sex were kept in Iowa, but fragments were obtained from the trappers employed by the state. The sex ratios obtained in the birds taken appear in Table 13.

All these birds were "shined" by auto headlights at night. The birds were taken "as they came" except in 1926–7 in South Dakota, when some hens were "passed up," hence for this year the probable actual ratio is higher on hens than the observed ratio. It is probable that hens are captured more readily than cocks by this method. The game wardens doing the work report that the cocks often flush but the hens do not. Furthermore when the cock escapes beyond the zone of light he keeps going, but the hen does not. In general, these "shining" ratios, therefore,

TABLE 13

SEX RATIO OF "SHINED" PHEASANTS

Year	State	No. of Birds	Cock:Hen Ratio of Birds as Taken	Previous Cock Law
1926-7	South Dakota	10,000	12:88	2/7 hens allowed
1929-30	South Dakota	12,000	25:75	1/5 hens allowed
1930-31	North Dakota	10,382	40:60	no open season
1930-31	Iowa	1,275	30:70	no restrictions

may show fewer cocks than actually exist on the ground. This error is probably constant, so that within a given state "shining" ratios kept over a period of years may be used to portray trends in composition of populations.

The variations between years and between states seem to fit the shooting differentials in the last column on the right.

Wight's (1930) observations on pheasants in Michigan would indicate a sex ratio somewhere around 1 cock: 1–2 hens. This is inferred from his statement that the "harems" rarely exceed 2 hens. If there were more hens, the harems would presumably be somewhat larger.

It may be noted in passing that even in states which do not restrict the killing of hen pheasants, shooting exerts a differential pressure against the cocks, by reason of the shooting ethic which causes the sportsmen to prefer cocks. Thus in Iowa during the open season of 1931, 182 reporting parties bagged 4124 pheasants, the sex ratio of which was 10 cocks to 6.4 hens, in spite of hens being legal game and considered easier to get.

Waterfowl Sex Ratio. We have in this subject an almost dramatic example of how the growth of thought in game matters is liable to take place along lines comparatively irrelevant to conservation. The volume of printed fact and opinion on waterfowl emerging during the last decade could be measured by the ton. Yet it was not until Lincoln compiled *The Sex Ratios of Banded Ducks* in 1932, that the possibility of a disturbed sex ratio, as a factor in the current waterfowl shortage, was even mentioned.

Lincoln finds that ten of our main species, of which nearly 50,000 individuals were banded during the last decade at 50 stations widely scattered over the continent, all show a preponderance of males. In all but three species (mallard, black duck, and woodduck) the preponderance runs 60: 40 or higher. The details appear in Table 14, which is reprinted from *American Game:*

TABLE 14

SEX RATIOS OF BANDED DUCKS

Species	Males	Females	Percentage Ratio
Mallard	12,386	9,572	56:44
Black Duck	477	344	58:42
Baldpate	413	251	62:38
Green-winged Teal	357	95	79:21
Blue-winged Teal	765	411	65:35
Pintail	6,308	3,759	63:37
Wood Duck	391	367	52:48
Canvasback	226	127	64:36
Lesser Scaup	2,633	1,444	65:35
Ring-necked Duck	455	123	79:21
Totals - - -	24,411	16,493	60:40

Some banding stations during particular years show a preponderance of females, but these exceptions may be ascribed to differential sex migration (Leopold, 1920), and to chance.

Lincoln thinks that the traps used for capturing ducks for banding, if selective at all, favor the capture of females.

All of Lincoln's evidence points toward the existence of a seriously deranged sex ratio. How long it has existed, or what causes it, remains unknown. It is barely possible, of course, that it always has existed, and represents a normal condition, but this seems improbable, especially in a group of species less strongly monogamous than most other birds. The reader should note that here again we have an excess of males associated with a known decline in population, and a known trend toward adversity in recent climatic and range conditions.

Grouse Sex Ratios. A heavy excess of males is definitely known to have been associated with the decline of the heath hen and possibly represents the final cause of the decline. The single bird now surviving is a male. The last female definitely recorded in the reports occurred in 1926 (Gross, 1928*c*, 1929).

An apparent excess of males has been recorded as often accompanying the cycle-troughs in ruffed grouse, and Schmidt (unpublished) finds an apparent excess of males in Wisconsin pinnated grouse but not in sharptails.

The association between decline and male-excess again seems to hold.

Deer Sex Ratios. Several tallies of deer seen on the range have been made, but they all have one defect in common: the yearlings are tallied as does (or else as fawns), hence the resulting figures do not quite give a sex ratio. The greater ease with which does and yearlings are seen probably further distorts the figures.

The sportsmen of Silver City, New Mexico, in co-operation with the Forest Service and the State Game Department, have collected from hunters on the Gila National Forest since 1923 a tally of deer seen (mule and whitetail) during their hunts. Of 115,223 deer seen during the period 1923–27, 64 per cent were "does" (doubtless including most yearlings), 15 per cent were "fawns" (doubtless including some yearlings), and 21 per cent were bucks. The percentages are consistent from year to year. After estimating various allowances and corrections, it is my opinion that the composition of this herd in 1923 just after the fawns dropped was as follows:

20%	bearing does (with 1.5 fawns each)	72% females 1 year and over
45%	dry does	
7%	yearling does	
7%	yearling bucks	28% males 1 year and over
21%	breeding bucks	
100%		

A one-buck law has always obtained on this range.

This composition and sex ratio was until about 1927 associated with satisfactory productivity, but subsequent history has indicated that it was leading toward an overgrazed condition accompanied by an as yet unanalyzed disturbance of productivity, possibly similar to that in Pennsylvania. Whatever the nature of this disturbance may be, it seems probable that it consists essentially of an abnormal percentage of females barren either through over-age, or short feed, or (less likely) buck-shortage, or all three. These eat up the range without producing killable stock.

An absolute tally of sexes was obtained when 22,362 mule deer were killed on the Stanislaus Forest in California, in 1924–5, during the process of stamping out the hoof-and-mouth disease. These deer, lumping all ages, ran 48 per cent male and 52 per cent female. A buck law had been in force for years, and productivity had been satisfactory. Unfortunately age-classes were not tallied.

Under the direction of Glenn Smith of the U. S. Forest Service, the fire guards in the National Forests of Montana tallied 12,531 mule deer in 1923–5. The tally showed, after throwing out 6709 deer of undetermined sex and age, 25 per cent bucks, 18 per cent does with fawns, 57 per cent "does." The last figure doubtless contains most of the yearlings of both sexes. One might assume these yearlings to be 14 per cent, as estimated for the Gila. This would leave 43 per cent dry does and 18 per cent wet does, or 61 per cent total does. The productivity associated with this widespread tally of a whole state had been various. A one-buck law was in effect.

In general, the excesses of females indicated in all these deer tallies are much larger than would be expected to occur in undisturbed mammal populations. Their abnormality is doubtless in part due to the selective removal of males through buck laws.

An abnormal ratio is of course not necessarily an unproductive one. Newsome advises 1 buck: 4 does as consistent with full productivity in wild whitetail. Oscar Johnson advises 1:5 for pheasants. These are doubtless just intelligent guesses, but they indicate how the ratio desirable in management of polygamous animals is always abnormally low in males. In English rabbit warrens the sex ratio is artificially altered to about one buck for each six or seven does (Haddon, 1931). Just *how* low males can be reduced without reducing productivity is a question not yet really answered for any American species.

In appraising the significance of sex tallies, the game manager should be warned against small samples, in which the laws of chance may cause an apparent distortion which does not exist on the ground. Obviously the probability of such false distortion decreases as the size of the sample increases. As a general rule of thumb, samples of less than 100 animals may be considered as of doubtful sufficiency.

Non-breeding. It is commonly assumed, in calculating rates of increase or percentage of nesting and juvenile mortality, that all stock mates and breeds provided it be not too old, too young, or too poor in physical condition, or provided it be not prevented from breeding by some distortion of the sex ratio in relation to its mating habits. It seems doubtful whether this assumption is tenable. In fact, "deliberate" non-breeding may often be one of the large "leaks" which prevent the realization of the apparent breeding potential of the species.

This question is still conjectural, however, because we know so little about breeding age, breeding condition, sex ratio, or mating habits, that we cannot say what degree of non-breeding they suffice to account for. All that can be said is that the apparent proportion of non-breeders in many species seems greater than would be accounted for by our available criteria of these conditions. In waterfowl and shorebirds, for instance, ornithologists have long since learned that the mere presence of a species during the breeding season by no means constitutes evidence that it is breeding. The nest or young must be adduced as evidence. Are these non-breeders all cripples? Are they non-breeding yearlings, *i. e.*, does the two-year minimum breeding age prevail among more species than we know about? In bobwhite, the ubiquitous unmated cock so frequently mentioned by Stoddard seems more numerous than the 53:47 ratio found by him, or the 52:48 ratio found by the Game Survey, would lead one to anticipate. The 45 per cent of dry does estimated to exist in the Gila Forest is hard to ascribe wholly to superannuation, while the 21 per cent of bucks would seem to exclude buck-shortage as a probable cause.

McLean (1930) and other writers definitely assert that "during dry years California and valley quail do not nest in large numbers and locally perhaps not at all." This assertion is intended to apply not only to the coveys of apparently superannuated birds already mentioned, but to the population as a whole.

E. A. Goldman tells me that during drouth years in Mexico he observed that local ducks did not breed until the rains came.

Non-breeding or deferred breeding in gambel quail during drouth years in Arizona has already been mentioned in Chapter II.

In short, there is evidence that extreme temporary adversity in weather or environment defers or prevents breeding to a degree sufficiently extreme to enable ordinary observation to detect it. Is it not a reasonable inference that lesser degrees of adversity cause lesser degrees of non-breeding, which are invisible to ordinary observational methods, but which, being more frequent, greatly affect productivity and population trends?

Conversely, has any life-history investigation encountered positive evidence that reproduction is universal among adults? I think not. To be sure, if non-breeding is important, European investigators, working through a longer period of time, might have been expected to discover it. It is not, to my knowledge, mentioned. Nevertheless, taking the available evidence as a whole, I am led to suspect that non-breeding is an important but so far unmeasured "leak" in certain times, places, and species.

It seems probable that where this condition exists it is caused by a deficiency in some obscure physiological stimuli associated with food, weather, density, or sex ratio. The discovery and control of such stimuli are of obvious importance to management. Some suggestive approaches to this question may be deduced from the closing chapters of Allee, 1932.

Hybrids. Two American game species are extensively hybridized—the pheasant and the bobwhite. Our pheasant is a mixture of long standing between various Asiatic species, principally the two subspecies *Phasianus colchicus colchicus* (Blackneck) and *Phasianus colchicus torquatus* (Ringneck).

Our bobwhite has been more or less hybridized by introductions of the Mexican subspecies (*Colinus virginianus texanus*) especially in New England, Pennsylvania, and Illinois, and the South.

Geneticists find that when birds are hybridized, there is an excess of males in the progeny at birth. The wider the cross the greater the excess (Crew, 1927; Thomas and Huxley, 1927).

Hybridized mammals, on the other hand, produce an excess of females. In the case of mammals this excess was predicted by geneticists (Haldane, 1922), on theoretical grounds before its existence was verified in mules (Craft, unpublished).

These disturbances of the normal sex ratio in hybrids have been found to recede with successive generations. Whenever *new* releases of Mexican quail, and releases of new races of pheasant are made, a *greater than normal excess of males* may, on theoretical grounds, be expected to follow for a number of generations. It is barely possible that it is great enough to injure productivity.

Inbreeding. Game management throughout the world seems to proceed on the assumption that game, especially gallinaceous birds, deteriorate if allowed to inbreed. A considerable part of the annual investment in management goes for trading eggs, introducing "new blood," and other measures aimed to prevent inbreeding. Shooting is regarded by laymen as a benefit to productivity because it disperses family groups and thus prevents inbreeding.

Like most traditional beliefs, these assumptions probably had their origin in observed behavior—presumably the observed productivity of game populations following releases of outside stock, or following shooting, as compared with the productivity of unmixed or unshot populations. It may be the old fallacy of assuming that when two phenomena are *associated*, they must be cause and effect. The assumption in this case is so widely entertained that a critical examination of its credibility is highly necessary.

No one knows the answer, because no actual controlled inbreeding experiments have ever been conducted on a wild animal. The work of geneticists on domesticated animals indicates no deterioration through inbreeding except where similar defects exist in both parents. Domestic varieties are often hybridized and seldom subjected to the rigorous selection incident to wild survival, therefore the frequency of variation (or defect) is greater than in wild species, therefore the probability of similar parental defects is greater than in wild species, therefore the probability of deterioration through inbreeding is greater than in wild species.

All this is merely another way of saying that wild animals are of relatively pure strain. The purer the strain, the less the chance of deterioration through inbreeding. Genetic principles, in short, tend to run counter to the popular supposition that inbreeding of wild game is injurious.

Game research, furthermore, tends strongly to show that inbreeding is rare, even in unshot populations. Stoddard (p. 169) and Price (1931) have shown that the "family group" is largely a myth in at least two species of quail. The *Game Survey* (p. 49) shows a "fall shuffle" in bobwhite which would tend to break up any such groups. Bracher (1931) cites suggestive evidence that pairs of Hungarian partridges (the only other American game birds except geese known with certainty to be monogamous) do not reunite in subsequent years. The probability of frequent inbreeding or unbroken family groups in the polygamous birds and mammals, and especially in the polygamous migratory birds, seems very remote, even where no shooting takes place. One must conclude that the probability of inbreeding in ordinary game populations is low, whether or not they are artificially mixed by shooting.

Isolated populations, or new establishments of exotics starting from a small initial stock, offer a greater probability of inbreeding, but the latter are sometimes notoriously productive, as witnessed by the rabbit in Australia, the partridge in Alberta, and the pheasant in South Dakota.

What observed phenomena, then, could have been misinterpreted to give rise to inbreeding theory?

The most probable is the well-known genetic phenomenon of hybrid vigor. Imported stock, even of the same species, is likely to represent a geographic strain slightly different from the native strain. Crossing of differing strains, races, subspecies (or sometimes even species, as in the case of the mule) is well known to induce abnormal size and vigor *in the first generation*, followed by a corresponding tendency toward debility or defect *in succeeding generations*.

Another possibility, suggested by the *Game Survey* (pp. 127–129) is the so-called Nutritional Hypothesis. This would apply only to species planted as exotics outside their natural range. Enhanced productivity, according to this hypothesis, might follow the introduction of "new blood," not because of any genetic influence, as popularly supposed, but because the "new blood" would bring with it transmissible reserves of certain minerals or vitamins lacking in the new range. It may be significant that the pheasant is probably an exotic in Europe, while the partridge is possibly an exotic in Britain. These countries and these species are, as nearly as now known, the origin of the inbreeding theory.

The frequent continuance of productivity in the bobwhite in spite of moderate shooting, and his failure to increase (on saturated range) in the absence of shooting, so often cited in support of the inbreeding theory, is by now clearly known to be a phenomenon of saturation point (see Chapter III). No genetic assumptions are necessary to explain the facts so far observed.

Maxwell (1913, p. 200) cites one estate owner who applies wild management exclusively to his pheasants, and who deliberately refrains from importing new blood "believing that you thus obtain a race which is most fit for the conditions prevailing in the locality."

Until scientific experiments have thrown more light on it, the game manager would do well to be cautious about investing in measures based solely on the inbreeding theory. Let him not forget that innumerable caravan of generations which "inbred," without benefit of gunpowder, through the still lapse of ages before the white man came.

FLOCK ORGANIZATION

European sportsmen have a separate name for the aggregations of individuals formed by each species of game. Thus one sees a *skein* of geese, a *whisp* of snipe, a *spring* of teal, a *company* of widgeon, and a *sord* of mallards. But the *skein* becomes a *gaggle* when on the water, while the *sord* becomes a *paddling*. What these become when on a stubble the deponent (Duncan and Thorne, 1912, p. 18) sayeth not.

This elaboration of sporting nomenclature is picturesque, and the correct usage of it is doubtless a source of pride to the seasoned veteran, and of embarrassed confusion to the neophyte. It has this basis in truth: the reasons for the formation of a gregarious unit and the relations and permanence of its membership are probably seldom alike for any two species. But alas! they may also differ at various seasons for the same species. So we will adhere to the simpler American usage:

Flock: any aggregation of birds.
- *Covey* or *bevy:* a small flock of birds which "lie."
- *Pack:* a large compact winter aggregation, sometimes all of one sex.
- *Band:* a loose aggregation, sometimes all of one sex.

Herd: any large aggregation of hoofed mammals, or a detached population unit of hoofed mammals.

Except for horned game which offers visible distinctions of sex and age, we are largely dependent on banding for reliable knowledge of gregarious organization. Since banding has barely started, we know very little. I will review briefly only such recent findings as are likely to be not yet known to the well posted sportsman or the student of game, or the interpretation of which is of special moment to management.

Is the Flock a Family? There is a persistent assumption that the family or brood of the year constitutes the membership of the small flock or the covey.

Affirmative evidence that the family constitutes a unit which persists for the year is strongest in the geese (Miner, 1923, pp. 114, 115, 121; McIlhenney, 1932, p. 300). Large flocks of geese are probably aggregations of families.

Evidence that the family breaks up almost as soon as it can fly is accumulating for at least some of the ducks. Thus a brood of black ducklings banded in Michigan July 30 showed simultaneous returns from both Michigan and Iowa on opening day, and on October 19 a return from Illinois (*Michigan Report, 1929–30*, p. 282). The fact that the fall migration of mallards sometimes shows one sex many days in advance of the other (Leopold, 1919) is in itself proof of early disruption of the family unit. The quick disruption of large flocks of arriving mallards into very small widely scattered aggregations—often singles and pairs—of "using" ducks, is familiar to every duck-hunter. The probabilities are that all duck flocks are temporary units of convenience.

Proof of a gradual but complete dissolution of the family unit is presented by Stoddard (pp. 169–172) for bobwhite:

> "Banding proves that in late summer and in fall quail coveys may be composed of one to three pairs of adults and their surviving young, with the addition frequently of one to several unmated cocks, or of pairs that failed to bring off broods. Young . . . that get lost from their own covey readily take up with another. . . . Birds scattered by shooting or by natural enemies are apt to encounter and join other aggregations . . . the greater the abundance, the more mixed is the relationship. . . .
>
> "The combining of broods . . . takes place at any time in summer or fall. . . . Though there is some joining together of surviving members of coveys all winter, this is most pronounced from midwinter to pairing-off time.
>
> ". . . every member of a covey . . . may wander away during the nesting season; . . . the covey occupying the range during the following winter is made up of birds of neighboring coveys and their offspring. . . . At best, only a very few birds of any covey occupy the same range from year to year."

Errington's more limited banding studies in Wisconsin confirm Stoddard's findings, except that his coveys, being more isolated, showed essential stability in location and membership during the winter season. In fall and spring, however, and also at the onset of starvation, they showed the same tendency to mix or move.

Hungarian partridge coveys are probably similar in organization to northern quail. The winter coveys are more stable in membership than southern quail.

The pheasant in Michigan, according to Wight (1931, p. 224) retains the brood unit up to the time of fall dispersal. The cock may accompany the brood up to the August moult. By the time of the hunting season the broods seem to have broken up into small loose groups of mixed sex and age.

Sex Bands and Packs. In Iowa, simultaneous with the hunting season in early November, there is a marked tendency for these pheasant groups to segregate into *loose bands all of one sex*, and these sex bands may persist through the winter.

Prairie chickens and sharptail coveys are probably broods or combinations of broods up to November. In November the prairie chicken, in particular, tends to form the large winter aggregations called packs. This is also the season when the chicken may migrate. Cooke (1888, p. 105) found the migrant chickens to be all females. The residual winter packs were all males. Whether this is still true, and whether winter packs commonly still found where chickens are not known to migrate constitute sex segregations, is not known. In Wisconsin packs as large as 1500 birds are reported (*Game Survey*, p. 178). It is definitely known, however, that as soon as booming commences in late winter, the males of both species are in separate flocks, each flock resorting to its own booming ground. Some booming grounds are simultaneously used by dancing sharptails and booming chickens. Schmidt (unpublished) suspects that in chickens colonization of new range is accomplished by the establishment of a new booming ground by a flock of males, which booms year in and year out until females arrive.

In ruffed grouse the brood unit seems to persist until the "crazy season" in October, after which small loose groups prevail until winter. In winter there is a tendency for ruffed grouse to form larger packs.

Turkey flocks are probably family units, at least in early fall. The gobblers form packs from nesting time until the young are two-thirds grown (Quarles, 1918). There is a never-to-be-forgotten picture in my mind: a pack of 30 gobblers which I met in the pine woods while cruising timber in Arizona. It was a sparkling morning in the full glory of the mountain summer. They filed by at 15 feet. I thought of Whitman: "Pride becomes him well."

Communal Bands. Gambel quail display the same tendency for winter coveys to combine already noted by Stoddard for bobwhite, but the combinations are larger and temporary, and split up into normal coveys before nesting begins. Gorsuch (1932, MSS.) says of southern Arizona:

> "Sometime in December the first of the plants termed winter annuals appear. This signals the consolidation of coveys into . . . communal bands. Coveys . . . unite to form bands of from 30 to several hundred birds. While so united the cocks and hens, if not already mated, choose their mates, and when not eating spend their time in courting antics. These bands last from two weeks to a month, and as they disperse the cocks go either . . . to the hen's covey range, or the hen goes with the cock to his. If the mating has advanced far enough the pair may go to a new range to nest . . . thus establishing another covey range."

Price (1931), in his careful study of flocking in the California quail, reports nothing to correspond with the large temporary bands of gambel, but his findings on flock organization otherwise agree with those implied by Gorsuch: the covey range is stable as in bobwhite, but the covey membership is much more so. There is no complete disruption of the covey during nesting,—only a slight loosening of range boundaries and an interchange of individuals.

Gregarious phenomena in big game are described by Seton and others, and will not be reviewed. This sketch of the game birds is far from adequate, but the main point is probably clear: there are many kinds and degrees of flocking, and field observations can be interpreted only to the extent that the flocking habits are known.

To know the flocking habit is easier than to explain its "survival value" or other cause for being. Allee (1932) suggests some intriguing physiological aspects of animal aggregation: Groups of fishes learn more quickly than singles. (Is the covey a school?) Grouped tadpoles regenerate lopped tails more quickly than singles. Fruit-flies grow larger and live longer in medium than in high or low density. Flour-beetles reproduce faster at first in a medium density than in a higher or lower one. Water slightly polluted by others of their kind has beneficial effects on certain worms, and in certain other lower organisms crowding affects the sex ratio. The game manager will do well to ponder these first fruits of a still virgin field of inquiry.

Summary. Each species has a characteristic mobility or cruising radius. The annual radius varies from a few hundred yards to nearly half the circumference of the earth. The utility of refuges and the minimum range unit habitable for a species both increase with mobility.

A given species is most mobile toward the edges of its range.

Low mobility is often associated with saturation point; high mobility with cycles.

Each game bird has a characteristic flight limit.

The spread rate of expanding populations was 5 miles per year in Lake States prairie chickens, 28 miles per year in Canadian Hungarians, 50 miles per year in starlings.

Tolerance of variation in the composition of habitable ranges is greatest near geographic optima. Some species under economic pressure have invaded new range.

Inter-species tolerance probably decreases with increasing density, and may be largely a matter of food competition.

Transplanted birds show six types of response to their new environment, varying from failure to success. Success is often determined by invisible factors. The pheasants, quails, and partridges transplant much more easily than grouse.

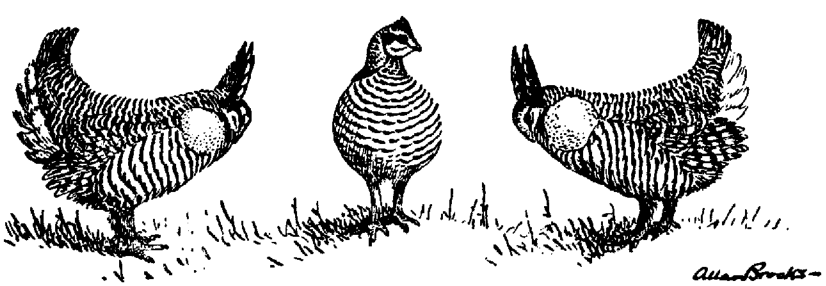
Game birds vary greatly in susceptibility to domestication. The biological distribution of this property tends to parallel the previous one.

Sex habits are imperfectly known, and may not fit the sex ratio. The sex ratio of game species at birth is unknown. The ratio at birth is modified by later mortality. A preponderance of males is found in many game birds, especially in adverse environments. A preponderance of females is found in mammals selectively hunted for males. Adverse environment may defer or reduce breeding.

Natural mobility tends to prevent inbreeding in game. Inbreeding is not known to be injurious to wild species. The tradition that shooting benefits game by preventing inbreeding is not yet supported by evidence.

Flocks vary in stability. Broods remain intact only in geese. Sex packs are common in grouse and pheasants.

The game manager who observes, appraises, and manipulates these half-known properties of mobility, tolerance, and sex habits of wild creatures, is playing a game of chess with nature. He but dimly sees the board, the men, or the rules. He can be sure of only two things: for intricacy and interest, any other game pales into insignificance; he must win if wild life is to be restored. If any braver challenge inheres in any human vocation, it takes something more than a sportsman to see it.



Chapter V

GAME RANGE[1]

What Is Game Range? When the game manager asks himself whether a given piece of land is suitable for a given species of game, he must realize that he is asking no simple question, but rather he is facing one of the great enigmas of animate nature. An answer good enough for practical purposes is usually easy to get by the simple process of noting whether the species is there and ready, or whether it occurs on "similar" range nearby. But let him not be cocksure about what is "similar," for this involves the deeper questions of *why* a species occurs in one place and not in another, which is probably the same as why it persists at all. No living man can answer that question fully in even one single instance.

It should be realized, first of all, that the present boundaries of the ranges of our present species constitute a great maze of diversities. If all species boundaries were plotted on a great map of the world, it would look like a wide pavement on a wet morning, after thousands of earthworms had been crawling over it all night, inscribing their irregular tracks.

Secondly, although the boundaries of these present ranges seem so stable to us that we record them in books and maps as fixed facts of nature, they have as a matter of fact undergone continuous change through the ages, each change constituting the response of the species to some change in its environment or in itself. Grinnell, in his essay "Presence and Absence of Animals" (1928) portrays with classical lucidity this march and countermarch of wild-animal armies across the long battlefield of time. A species, he says, does not shift or wander; it is *herded about* by the compelling orders of circumstance. It survives only where and when it finds an "ecologic niche," or "set of conditions which provide adequate means of subsistence for the particular species, and which that species can tolerate."

[1] Parts of this chapter appeared as an article in *The Journal of Forestry*, Vol. XXIX No. 6, October, 1931.

Friedman (1931) describes the interplay of factors determining "range" in terms of an elaborate analogy:

> "We may . . . compare . . . the distribution of birds to a symphony played by a great orchestra. . . . Each instrument . . . is . . . one factor . . . in the environment. . . . At any one moment the individual sounds . . . of the many instruments . . . fuse and blend to form one auditory effect. This is comparable to the range of one species (at any one time). No two instants are exactly alike in their sound summations, just as the distributions of no two species are ever wholly similar. In the production of certain sounds all the instruments may be combined; in others, only certain ones; in others, two of the component sounds may be mutually interfering and obliterate each other. In other words . . . each present distributional fact represents a polyphony of causes."

The game manager seeks to alter *one* of the sounds for *one* geological instant for the benefit of man. He seeks to make one biologic niche a little more tenable than that resulting from the "fortuitous concourse" of man and nature.

How shall he go about it? He cannot really understand "the polyphony of causes" which determine the range (and abundance) of a species, but he can manipulate the more obvious features of the environment with at least partial intelligence by comparing them with what determines *his own* range and abundance.

He can postulate, for instance, that for a piece of land to be habitable by game it must offer places suitable for feeding, hiding, resting, sleeping, playing, and raising young.

The essential difference between a deer and a man is that man builds farms, factories, and cities to provide himself with the elements of an habitable range, whereas a deer must accept the random assortment laid down by nature and modified by human action, or move elsewhere.

In both cases that endless competition which we call society consists essentially in a struggle for the best assortment of places to feed, hide, rest, sleep, play, and breed.

If the assortment of environmental types in any one locality falls short of being adequate to maintain thrift and welfare, the species shrinks in numbers to what the locality will support. When such shrinkage approaches zero, the locality is lost altogether, and the species withdraws. When such withdrawals become too prevalent, the species becomes extinct.

Environmental Types. Each species requires its own assortment of specialized places. In our present state of almost total ignorance we can list and classify these places only in the most general terms. We call them, collectively, food and cover. We often think of food and cover needs as a constant property of the species, with no variations in time. Yet a little observation shows at once that the needs of each species vary greatly according to season and circumstance. The menu of most animals would look like an almanac—a new set of foods for each month of the year. Likewise their enemies and their coverts.

In the north temperate zone nearly all species have two critical seasons; one, the season of winter storms, and two, the breeding season. Many game ranges are adequate for more species or greater densities than now inhabit them, but for particular deficiencies during these critical seasons. The practical problem of game-range management, therefore, may be approached and examined from this standpoint of critical seasons, and it can usually be assumed that all other seasons and conditions are satisfactorily provided for.

In bobwhite quail, for example, in the northern half of the United States, feeding places are usually adequate except during winter snow or sleet storms. Under these conditions a cornshock, or a patch of seed-bearing ragweed protruding above the snow, is a requirement for survival, *i. e.*, is the critical element in the food factor for northern bobwhites.

Places to hide are likewise usually adequate except during winter, when the white snow buries the understory of grass and leaves and renders every bird visible to predators. Under such conditions the mechanical protection offered by a thorny bush like osage, or a dense tangle of grapevines, represents the quail's only chance to dodge his enemies.

As nearly as we know, almost any ground will do for resting purposes, except during winter snows, when there must be a hiding place near at hand in which the birds may seek refuge from sudden attack.

For a sleeping place quail require at all seasons a rather open and preferably elevated spot, from which, if attacked at night, they may successfully take wing without striking mechanical obstacles.

If the quail requires a special place for play, we have no knowledge of it.

For nesting, quail require moderately thin grass or brush on a well-drained spot, with bare ground nearby on which the young may dry out after rain. Stoddard thinks this accounts for the frequency with which nests are found near paths and on roadsides.

Quail are commonly believed to require grit. If they do, then ledges of rock or gravel, or windfalls bearing gravelly soil, are necessary during snows.

Let us now contrast these environmental requirements with those of deer. In the Lake States a deer range requires first of all a cedar swamp which combines food and shelter for "yarding" during deep snow.

For hiding, a deer prefers an evergreen thicket on the point of a hogback or saddle, where one or two jumps will carry him out of sight, no matter from which direction an enemy approaches.

For resting, the requirements are similar, except that during the fly season an open and preferably elevated place is needed in order to obtain the assistance of the wind in fighting insects.

For sleeping, the requirements of the species are not radically different than for hiding.

For play, open places are needed.

For fawning, the doe prefers to be near water in order that she may satisfy the thirst consequent to nursing without undue expenditure of energy in travel.

Deer have a special requirement for salt, which should be available without undue travel.

These two illustrations will suffice to show that each species has its own particular set of environmental requirements, that there is usually a critical season during which each of these is most deficient, and that the probability of surviving this critical season depends on the availability of certain particular kinds of vegetation, topography, or soil, which are usually associated with certain vegetative types. In other words, a game range, to support a given species, must have a certain composition in which the essential environmental types are represented.

What Is a Type? The use of the terms "food" and "cover," while convenient categories for general discussion, carry with them a constant danger of loose thinking, which may lead the game manager into false or unsuccessful efforts to improve range. Just as "house" or "restaurant" are inclusive terms for hundreds of quite distinct human desires or needs or facilities, *not more than one of which may determine the whereabouts or welfare of a given person at a given time*, so the terms "cover," "food," and "type," fall far short of describing particular realities. A quail sits under a hedge of a snowy morning, not because it is "cover," but because a Cooper's hawk visited the covey yesterday, and this quail, fearing he may call again today, has need of the protecting thorns. For another enemy he might seek another kind of cover. Like as not he has selected the particular part of the hedge with the hawk in "mind." A prairie chicken may perch on the same hedge for an entirely different reason—to get the early sun; a rabbit for yet another—to dodge a fox. So with food. A covey of quail is in the oak woods, not because they need oak woods as such, but because a squirrel has been dropping acorn crumbs from a particular oak. A grouse brood seeks an aspen ridge out of no interest in either aspen or ridges, but because it is the place to seek an ant hill for "eggs," or to seek a dust bath, as the case may be. This is enough to show the point: the service rendered by any environmental type not only varies by species and season, but is *likely to be contained within a very small fraction of the type*. We must understand something of what these services are before we know what a type is, and the same "type" may mean wholly different things for different species.

Interspersion of Types; Relation to Mobility. A city includes all of the environmental "types" which human animals require for thrift and welfare. If, however, all the kitchens were situated within one quarter of a given city, all the bedrooms in another quarter, all the restaurants and dining-rooms in a third, and all the parks and golf courses in the last quarter, the human population which it would be capable of supporting would be considerably reduced. The extent of the reduction would vary inversely to the mobility of the inhabitants. In fact, it is only the recent artificial extension of the human cruising radius by means of mechanical transportation that would allow such a city to be inhabited at all.

Likewise with game. The game must usually be able to reach each of the essential types each day. The maximum population of any given piece of land depends, therefore, not only on its environmental types or composition, but also on the *interspersion* of these types in relation to the cruising radius of the species. Composition and interspersion are thus the two principal determinants of potential abundance on game range.

The environmental requirements of quail, for instance, are associated with four principal environmental types, namely woodland, brushland, grassland, and cultivation. If a square mile of quail range consisted of 25 per cent each of these types, it would probably offer somewhere near optimum composition.

If, however, each 25 per cent lay in a single solid block of 160 acres, it is quite probable that the square mile would support only one covey of quail, and this covey would be located *at the juncture* of the four types. This would be the only place where a bird of short cruising radius could reach each essential type each day. In other words, the juncture of the four types would offer that combination of composition and interspersion which constitutes a range for game of low mobility.

If, however, a square mile of land of the same composition had its types so interspersed as to offer many places where quail could reach each of the four types each day, it would support many coveys of quail instead of one. This effect of interspersion is illustrated in Fig. 9.

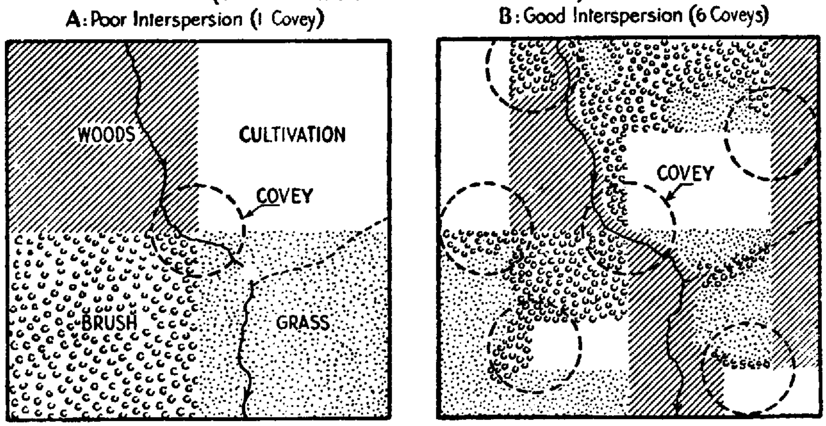
Management of game range is largely a matter of determining the environmental requirements and cruising radius of the possible species of game, and then manipulating the composition and interspersion of types on the land, so as to increase the density of its game population.

In Europe, some game ranges are further manipulated to make the shooting more convenient. Maxwell, for instance, shows by elaborate diagrams how to arrange the cover on a pheasant range so as to get a good "rise" (flushing ground) for the birds after the drivers have concentrated them in one covert, and how to arrange the rise and the covert so that they will fly high and fast over the line of waiting guns. It may be doubted whether we are ready for such technique in America; certainly not until we have restored a game supply.

Tolerance of Variation in Composition and Interspersion. The number of environmental types required by a given species varies greatly according to the refinement and accuracy with which the types are defined. Thus quail might be said to require from 4 to 40 types for a unit range, depending on the degree to which each

Fig. 9

INTERSPERSION OF TYPES - RELATION TO MOBILITY & DENSITY OF QUAIL
(SAME TYPES AND SAME TOTAL AREA OF EACH)



is split up and delimited. Since we are here trying to illustrate principles rather than deal with the detailed biology of game species, the simpler classification will suffice quite as well as the more complex. We may conclude that quail ordinarily require woodland, brushland, grassland, and cultivation for an optimum unit range. In special cases, however, one, two, or even three of these may be dispensed with, provided the remainder be of the right kind and in sufficient quantity. Thus in the Ozarks some quail inhabit a range composed entirely of woodland, but only when the woodland is open enough to offer the brush, grass, and weeds characteristic of the other three types. Furthermore, such "woods quail" exist only in relatively thin populations. In short, the exception may be said to prove the rule that quail have four essential environmental types.

On the other hand, in Kansas, fairly dense quail populations occur on some ranges entirely devoid of either timber or brush. The grass and weeds are so vigorous, however, as practically to constitute brush, while the kaffir corn and wheat fields offer exceptionally abundant food. No real exception to the quail's ordinary requirements seems to be involved.

Some species attain normal populations in ranges composed of one or, at the most, two types. Thus antelope characteristically inhabit range composed entirely of grassland. They will accept, however, ranges composed of up to 50 per cent woodland, provided this be open. There is evidently a shelter, and possibly a browsing, requirement during winter storms, which is associated with either woodland or rough topography.

While we are only at the threshold of an understanding of the ecology of game species, it may be said that each species requires from one to four environmental types on each unit of habitable range, and that most species require three or four.

Game as an Edge-effect; Law of Interspersion. The preceding caption asserts, in effect, that game is a phenomenon of *edges.* It occurs where the types of food and cover which it needs come together, *i. e.*, where their edges meet. Every grouse hunter knows this when he selects the edge of a woods, with its grape tangles, haw-bushes, and little grassy bays, as the likely place to look for birds. The quail hunter follows the common *edge* between the brushy draw and the weedy corn, the snipe hunter the *edge* between the marsh and the pasture, the deer hunter the *edge* between the oaks of the south slope and the pine thicket of the north slope, the rabbit hunter the grassy *edge* of the thicket. Even the duck hunter sets his stool on the edge between the tules and the celery beds. Wight finds that pheasants nest in the outer *edge* of the hayfield where it adjoins the fencerow; the Grouse Report finds that grouse nest on the *edge* where the young heather adjoins the old; Stoddard and Maxwell say that bobwhite and Hungarian partridge often choose the *edges* of open roads or trails for nesting. Even wild turkeys show a curious tendency to nest at the *edge* of trails. We do not understand the reason for all of these edge-effects, but in those cases where we can guess the reason, it usually harks back either to the desirability of *simultaneous access* to more than one environmental type, or the *greater richness* of border vegetation, or both.

It will also be observed that edge-effects are most numerous in game of low mobility and high type requirements. I know of few convincing instances where edges attract mobile, one-type game like geese, or buffalo, or antelope, or plover, or sea-ducks.

The linear mileage of type edges available in any block of range is, as a matter of geometry, proportional to the degree of interspersion. Case "A" in Fig. 9, for example, has two miles of edge within the exterior boundary of the map, while Case

"B" has ten miles. An acre of fencerow or hedge, consisting, so to speak, entirely of edges, usually has more game (and songbirds also) than many acres of unbroken woods, or wheat, or corn. Abundance of non-mobile wild life requiring two or more types, appears, in short, to depend on the degree of interspersion of those types, because this determines the length of the edges of those types, and this in turn their vegetative richness and simultaneous availability.

The same thing may be stated mathematically as a law of interspersion: *The potential density of game of low mobility requiring two or more types is, within ordinary limits, proportional to the sum of the type peripheries.*

I am not sure that the scientific ecologists know this law as well as woodsmen do. Texts on ecology all recognize that certain species are associated with certain types, but I have found few which recognize the need for diverse types in juxtaposition, and none which state clearly that the frequency of such juxtaposition depends on interspersion, or that interspersion determines population density.

A clear and condensed exposition of the ecologist's view of this question is given by Dice (1931*a*).

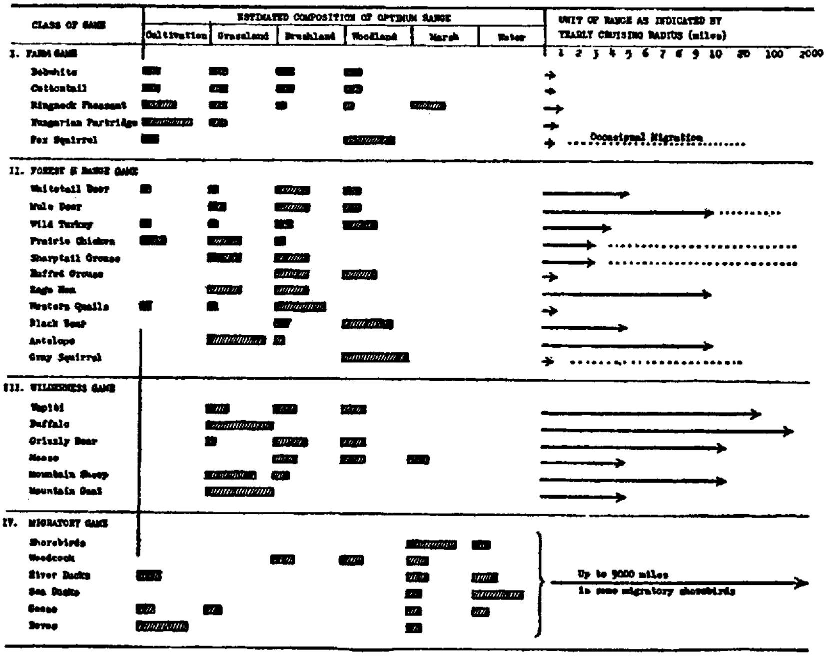
Classification of Game Species. With the foregoing background, it is now possible to suggest a classification of American game species with respect to their range requirements. Fig. 10 recognizes four classes: farm, forest and range, wilderness, and migratory game. These classes have been previously published and defined in the *American Game Policy* (1930).

Farm game consists of species which, because of their short cruising radius and high requirement for cultivated land, are especially adapted to be grown on farms. A glance at the chart shows that their cruising radius is usually much less and their optimum percentage of cultivation much more than that of the other three classes. The cottontail probably has the shortest cruising radius of any American game species, with bobwhite a close second. The Hungarian partridge undoubtedly tolerates the highest percentage of cultivation. All five farm game species are non-migratory and all but fox squirrels are non-cyclic. The fox squirrel is classified as farm game because optimum populations are obtained in woodland adjacent to cornfields.

Forest and range game consists of species inhabiting wild

Fig. 10

CLASSIFICATION OF AMERICAN GAME SPECIES



land but compatible with forestry or livestock operations. Many of them accept (and some of them thrive best under) a low percentage of cultivation. None of them thrive on continuous blocks of cultivated land, but on the other hand they do not require the opposite, or wilderness, condition. Deer, ruffed grouse, and wild turkey thrive best on forest land with a partial interspersion of cultivation. Pinnated and sharptail grouse thrive best on prairie or brush land with a partial interspersion of cultivation. Sage grouse, antelope, and western deer tolerate moderate grazing or forestry, even though wilderness conditions probably suited them best. The southwestern quails, here classified as forest and range game, might be classified as farm game, but for the high proportion of brush lands needed for optimum ranges. Black bear are obviously tolerant of civilization and belong in this class, except in a few cases where they conflict with special kinds of livestock or farming. Gray squirrels are included in this class because of their requirement for ungrazed woodland, which is usually not found in highly developed farming communities.

In short, none of the forest and range species are adapted to farms, but none require the exclusion of farming, grazing, or forestry.

Wilderness game consists of species harmful to or harmed by economic land uses, and therefore suitable for preservation only in special public game reservations, or in public wilderness areas. Elk and buffalo are in this class because they damage farms and compete with livestock; grizzly bear, moose, caribou, and mountain sheep because they usually fail to thrive in contact with settlement; mountain goats because they require a topography so rough as to be automatically wilderness.

Migratory game consists of species of such long cruising radius that they always leave the land on which they were raised. This class includes all the waterfowl and shore birds, and also the migratory doves and pigeons. Some migratory species, as for instance river ducks, geese, and doves, thrive best on a high percentage of cultivation on their fall, winter, and spring range. In the case of geese and ducks, however, this is not true of the summer or breeding range.

One may infer from these definitions that a certain degree of settlement actually improved the range for farm, forest, and migratory game, instead of deteriorating it, as is usually supposed. This inductive conclusion is emphatically supported by the historical evidence presented in the Game Survey, especially in the cases of bobwhite quail, pinnated grouse, and cottontail. These species attained an abundance in the early days of crude farming probably far surpassing that obtaining under pre-settlement or virgin conditions. The lack of productivity now characteristic of most of their ranges is not due to settlement and cultivation as such, but rather to overkilling, overgrazing, and clean farming. It is suspected that river ducks and geese likewise experienced a large increase with early settlements, but historical evidence is so far lacking.

Deer, sharptail grouse, and pinnated grouse likewise experienced a peripheral shift as settlement opened the way for them by converting Class III range into Class II, and closed the way behind them by converting Class II range into Class I. The northward shift of these species in the north central states is traced in the Game Survey.

Range Balance. The practical question of improving game ranges deals almost invariably with the same principle of *balance* already discussed in Chapter II in terms of factors. When we say that settlement opened a way northward for pinnated grouse by changing Class III range into Class II, we mean that it created artificial prairies and put a little grain in them, thus putting the food and cover factors *in balance* for this species. When we say that settlement evicted pinnated grouse from their native habitat by changing Class II range into Class I, we mean that intensive agriculture further increased the grain and decreased the prairie grass, thus throwing the cover factor out of balance with the food for this species.

Every range is more or less out of balance, in that some particular aspect of food or cover is deficient, and thus prevents the range from supporting the population which *the other aspects would be capable of supporting.* Management consists in detecting that deficiency and building it up. This once done, some *other* aspect will be found to be out of balance, and in need of building up. Thus, one move at a time, each skillfully chosen, does the manager attack the job of enhancing productivity. This will be further discussed in later chapters on food and cover.

The measurement of game range to detect differences in balance, and for other purposes, will be discussed in Chapter XV on "Miscellaneous Techniques."

Summary. A range is habitable for a given species when it furnishes places suitable for it to feed, hide, rest, sleep, play, and breed, all within the reach of its cruising radius.

Deficiencies in such places are usually seasonal. Management deals with offsetting them at the critical season.

Types of food and cover are the general components of the range with which the particular needs of the species are associated.

Carrying capacity in species of high type requirements and low radius, varies directly with the interspersion of the types, which is proportional to the sum of the type peripheries. Such game is an "edge effect."

Game species may be divided into four classes based in general on decreasing tolerance of or need for agricultural types, and increasing mobility: I, farm game; II, forest and range game; III, wilderness game; and IV, migratory game.

Game range management deals with keeping the range types in balance.

This completes our analysis of the theory of game management. Most of the pieces of which it is built are well known to biologists, and many even to laymen.

Let the reader understand, however, that the aggregate significance of these pieces is greater than their sum. They constitute the parts of a biological *engine*, which the techniques next to be described may *drive* if applied with sufficient skill. The fuel for that engine lies ready to hand—the inherent fruitfulness of the earth. The forces inherent in the juxtaposition of hydrogen and carbon, which we skillfully employ to do our heavy labor, are no more potent or useful than those which inhere in the juxtaposition of life and land.

We have so far explored the nature and properties of these forces. We have now to examine what rudiments of skill have been developed for their beneficial use.

PART II

MANAGEMENT TECHNIQUE


Allan Brooks

CHAPTER VI

MEASUREMENT OF GAME POPULATIONS; GAME CENSUS

Steps in Management. The preceding chapters have attempted to define the history and purpose of management, and to describe the biological mechanism which it seeks to conrtol, the properties of game species as related to that mechanism, and the classes into which game species and game ranges fall by reason of their different properties. These definitions and descriptions constitute the essential background of game management.

We must now deal with the methods by which the biological mechanism is to be controlled. These constitute the technique of game management.

The initiation of management on any piece of land usually involves four consecutive steps:

1. *Census.* Measuring the stock on hand.
2. *Measuring the Productivity* of the stock and comparing it with a standard.
3. *Diagnosis.* Weighing the factors and selecting one or more for control. Testing these on a small scale to verify whether the selection is correct, and the method of control effective.
4. *Control* of selected factors on a larger scale.

This chapter deals with the first step: the measurement of the stock.

Measurement involves more than mere enumeration or census. The composition and condition of the stock is often quite as important as its numbers, and may have a bearing on the second, third, and fourth, as well as on the first step in management.

Measurement of the volume and growth of forests, which is called forest mensuration and includes timber cruising, is the subject of dozens of volumes, both American and European.

The measurement of game populations is of equal complexity, but there is as yet little literature, except in the single field of bird banding. Hence this chapter can hardly hope to do mose than describe and organize typical fragments of the technique or far developed. No comprehensive treatment is as yet possible.

Kinds of Measurements. The enumeration of the population of a given area at a given time is properly called a game census. The determination of trends or fluctuations requires the census of a given area at two or more times. The determination of relative abundance involves the census of two areas at the same time. The determination of aggregate movements (migration) or individual movements (mobility) involves the observation and sometimes the measurement of aggregates or individuals at consecutive times.

In addition, the prescription of proper management measures involves the analysis and measurement of game populations in many ways, such as determining the composition in respect to sex and age, determining productivity, determining mortality from decimating factors, predicting the effects of environmental changes, and determining ratios between sexes, ages, and species. These are reserved for future chapters.

GAME CENSUS

Kinds of Technique. These measurements are made: (1) by direct enumeration of whole areas or samples of them, (2) by ratios based on trapping, banding, and later recapture of sample individuals, or (3) by indirect observation of the condition or density of populations through the use of indices.

When we count the deer tracks entering a yarding ground after the first deep snow, we get a census by direct observation, and we also get a population density provided we know the area of range served by the yard in question. Likewise when we count the coveys of quail on a farm by working it thoroughly with good dogs, we obtain a census by direct observation.

The technique of banding, it is hoped, requires no definition. Its use in game census will be explained later.

When we compare the quail populations of two areas by counting the number of coveys which the same dog can find in the same length of time, we are using an index, namely coveys-per-dog-per-day, as an indirect measure of, or index to, abundance. We must match out the weather, the season, the time of day, and the other variables which affect the validity of the comparison. Indices are useful short-cuts, but they are of no avail, and may lead to dangerous fallacies, unless the variables which affect their validity are matched out or at least recognized.

Census Standards; Sources of Error. For a game census to have maximum value it must adhere to certain standardized definitions, even though it cannot adhere to any standardized method. It should be clearly set forth, for instance, whether young animals less than one year old are included in the figures. It is a custom of long standing among stockmen in the West to exclude all livestock less than one year old from the enumeration or census of a range herd. When a cowman tells the bank he has a thousand cattle, he means a thousand cows, bulls, and yearlings, *plus* whatever calves of the year be on hand. Hence most western game men, especially in dealing with big game, exclude animals of less than yearling age. In birds, however, the young of the year are seldom distinguishable and often constitute the bulk of the stand. For this reason all census and density figures in this book include all ages.

It goes without saying that a census of resident game should always give the area to which it applies.

A frequent error in game census is to compare the densities of population on two tracts of radically unequal area without correcting for the "blanks" or vacant places which almost always exist in the larger area to a greater degree than in the small one. Census figures reduced to an area basis are misleading unless the areas are of comparable size or unless we know how to correct for blanks. Thus on areas of 40 to 160 acres, one quail per acre is a normal and satisfactory population, whereas on areas from a section to a township in size, lying in the same locality and representing the same conditions, a quail per 4 to 6 acres might be found. The reason for the discrepancy is that every township contains large areas of bare fields, continuous woods, or other types not inhabited by quail, whereas in selecting a smaller area, these blanks are unconsciously and automatically excluded. Elton (1932, p. 71) applies this same reasoning to census work in ants, but his terminology is different. A density derived from a census including blanks he calls "lowest density." A census excluding blanks he calls "economic density." A census on what is here called a temporary concentration he calls "highest density."

Another frequent source of error in game census is to ignore seasonal differences in population due to progressive mortality. Thus a November 1 count before the hunting season might show twice as many quail as a March 1 count made on the last snow on the same ground during the succeeding spring. In the British Isles spring census of breeding stocks seems to be standard. In America, unless otherwise specified, fall counts at the beginning of the hunting season are standard.

Unless the area on which the census is to be made is very small, the census must use samples instead of attempting a count of the area as a whole. These samples must either be selected so as to be representative of the whole, or they must be so numerous that their abnormalities will be averaged out. The accuracy of the census will depend on the number of samples, the skill with which each is selected, and the skill with which the enumeration of each is made.

Choice of Method. The method of enumerating the game, and the season of attempting it, must be adapted to the habits of the species. Some species, like quail and antelope, gather in coveys or herds of more or less fixed composition, and if these can be found on open ground, or can be flushed so as to be counted in flying, we have the simplest possible problem in census taking.

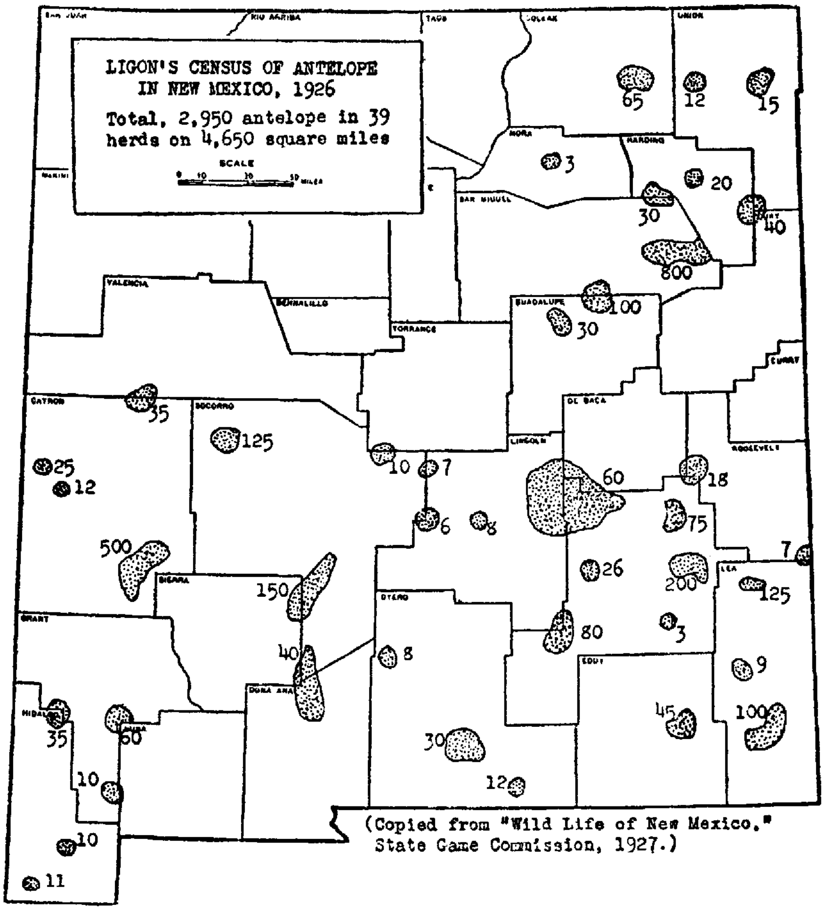
Those mammals which execute seasonal movements or migrations, such as the mule deer of Routt County, Colorado, and the caribou of the Barren Grounds, likewise present a simple census problem. They or their tracks can be counted at strategic points on the migration route.

On the other hand, migratory birds which do not assemble in fixed aggregations, or which move at night, and upland species like pheasants which seldom form coveys and which take refuge in swamps from which they cannot be flushed, or prairie chickens which assemble in shifting packs of unstable location, present the other extreme of difficulty.

Those who desire to review the zoological literature on choice of methods should consult Dice, who gives a clear comparison of the fundamentals of various census techniques for birds (1930) and for small mammals (1931*b*), and cites other authors who have described particular census methods both for animals and plants.

Direct Census. An example of direct enumeration of mammals which form detached herds of comparatively fixed composition is Ligon's (1927) census of antelope in New Mexico, illus-

FIG. 11



(Copied from "Wild Life of New Mexico," State Game Commission, 1927.)

trated in Fig. 11. Most of these herds are so small and isolated that the maximum number seen together at the inhabited spot constitutes a reliable census. The larger herds shown on Ligon's map, however, consist of overlapping groups, which can be counted only with the help of snow or by repeated observation.

The census shows 2950 antelope in the state, or 42 square miles per antelope. The actually inhabited range (area of stippled spots) is about 4650 square miles, a density of about 2 square miles per antelope.

Sometimes direct enumeration is possible in mammals which do not form fixed herds, but which are forced into the open during severe snows. Simultaneous counts on the open areas used during such periods constitute a dependable census. The co-operative Yellowstone elk count conducted at intervals since 1912 by the Forest Service, Biological Survey, and State of Wyoming, uses this method. Sheldon (1927) reports the counts from 1912 to 1927 as varying from 9346 to 19,493. The 1927 census, 19,238 elk, divided by the gross area of both the summer and winter range (roughly 3400 square miles) gives a population of about 6 elk per square mile, or 1 per 100 acres.

One of the simplest means of direct census is the covey count. For instance, McLean (1930) counted and mapped the coveys of California quail on a 22,000 acre tract of foothills in San Mateo County, California, during the winter of 1928–29. He found 75 coveys totalling about 2000 birds, or 1 bird per 11 acres.

Counts of coveys are practicable in quails because of the low mobility of the coveys. Herd counts are practicable in antelope, in spite of relatively high mobility, by reason of the wide separation of the herds. Birds which are mobile but scarce, and which exist in widely separated detached units, yield to a combination of the methods used by McLean and Ligon on quail and antelope respectively. Thus the Game Survey of Iowa (1932) mapped and (in most cases) enumerated each remaining remnant of resident prairie chickens in that state. It was necessary, however, to exclude *all winter observations* because of the annual influx of migrant chickens, which far outnumber the resident birds.

Direct enumeration, even of non-coveying birds, is often practicable by the skillful use of a bird dog. Thus Wight (1931*a*) made a dog-census of pheasants of the Northfield Refuge (600 acres) near Ann Arbor, Michigan, at various seasons for three successive years, and found fall populations of up to 300 birds, or 1 per 2 acres, although efflux or hunting each year reduced the winter population to 50 birds, or 1 per 12 acres.

In Europe red grouse, gray partridges, and pheasants are driven over the guns. Counts of the driven birds yield a direct census subject to only one error: the "leakage" of unflushed individuals. This leakage seems to be greatest in pheasants, and least in red grouse. The British literature indicates that in red grouse the leakage is negligible. An annual drive census, a direct count of spring breeding stock, and a kill record are often available for the same area for long periods of years.

For example: The average population of a typical 5000-acre English grouse moor under intensive management, as interpolated by Leopold and Ball (1931*a*), is 1200 birds, or 1 bird per 4 acres, in spring. It is 3700 birds, or 1 bird per 1.5 acres, at the beginning of the fall drives. In Scotland the average moor is twice as large but has about the same population, the density thus being 1 bird per 8 acres in spring, and 1 per 3 acres in fall.

The maximum fall population occurred on Broomhead Moor, 4000 acres. This small but excellent moor yielded, from 1908 to 1910, a grouse per 0.8 acres, indicating an apparent fall population of a grouse per 0.5 acres, or 2 per acre. The small size of this moor suggests that there may have been some influx to magnify this kill above the actual productivity of the moor.

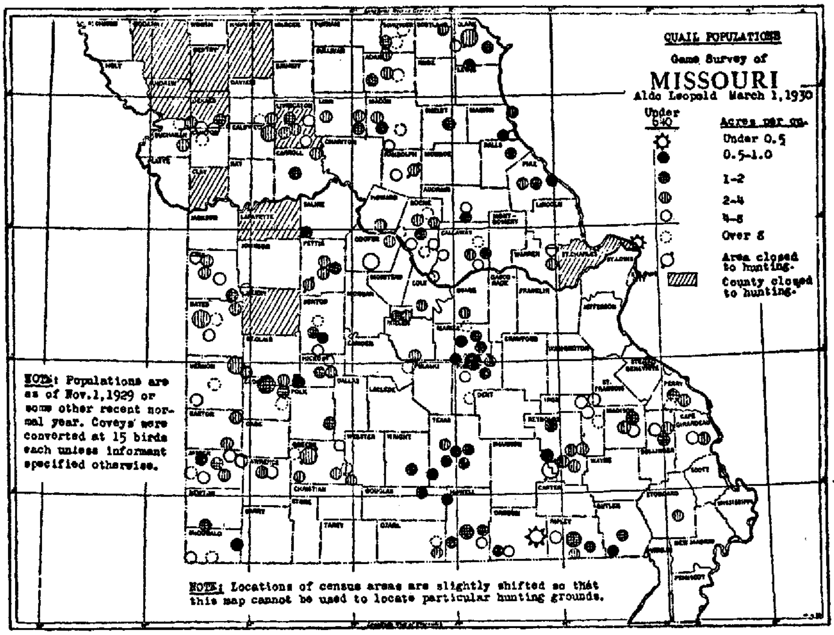
In gray or Hungarian partridge, Page (1924) gives the normal spring population on small English manors as 1 bird per 3 to 10 acres. This is derived from direct spring counts made by the game keepers. Maxwell (1911) says that on the average manor of 6500 acres the spring census usually ranges from 2 to 5 acres per bird, averages 4 acres, and never runs denser than 1½ acres or thinner than 10 acres.

By and large, complete and direct population counts are applicable mainly to large mammals, or coveying birds like quail or partridge for which dogs can be used to cover large areas in a short time, or to driven birds, like red grouse. Field trial grounds offer the most frequent opportunity for large-scale intensive census by dog work.

Census by Samples. Very large areas, of the magnitude of a county or a state, can only be censused by selecting representative samples. Making a census of the whole territory is usually prohibitive in cost.

An attempt to use the sample plot method on a large scale is Leopold's (1930) map of quail density in Missouri shown in Fig. 12. The objective in this work was to compare quail densities with cover and food distribution, rather than to enumerate

FIG. 12



METHOD OF CALCULATING CENSUS FROM ABOVE MAP

1	2	3	4	5	6	7	8
Density Class (acres per quail)	No. of Samples		Per Cent of Samples		Per Cent of State (acres) (total area x col.5)	Median Density (acres per quail)	Quail Population (6 x 7)
	On Map	Arbitrary Correction	On Map	Arbitrary Correction			
Under 0.5	1	1	0.5	0.2	60,000	0.4	150,000
0.5 - 1.0	14	14	8	6	1,800,000	0.7	2,000,000
1 - 2	42	42	23	18	5,400,000	1.5	3,600,000
2 - 4	54	54	31	23	6,900,000	3.0	2,300,000
4 - 8	42	60	23	26	7,800,000	6.0	1,300,000
Over 8 (assume 16)	24	60	14.5	26	7,800,000	12.0	650,000
Total	171	231	100	100	*30,000,000		10,000,000

*Actual area of 44,428,000 acres arbitrarily reduced for cities, water, swamp, and other uninhabitable areas.

the quail, hence no precautions were taken to get a true "cross section" of the state as a whole. If the plots had been distributed according to a geometric pattern, such as one plot in the middle of each township or each fifth township, they would have been representative of the state as a whole, and a census could have been derived from them. As a matter of fact, it is certain that low-density plots are under-represented on the map, due to the difficulty of finding farmers or sportsmen who had counted coveys on thinly populated samples.

Despite these defects, in order to show the *principle* by which the sample plot census method works, a sample census calculation is shown under the map, an arbitrary correction column being added to bring the density classes into some kind of correspondence with reality. Such a correction would, of course, not be necessary if the plots had been chosen for census purposes. It should be understood that the resulting figures, 10,000,000 quail, do not purport to be anything but illustrative of a method.

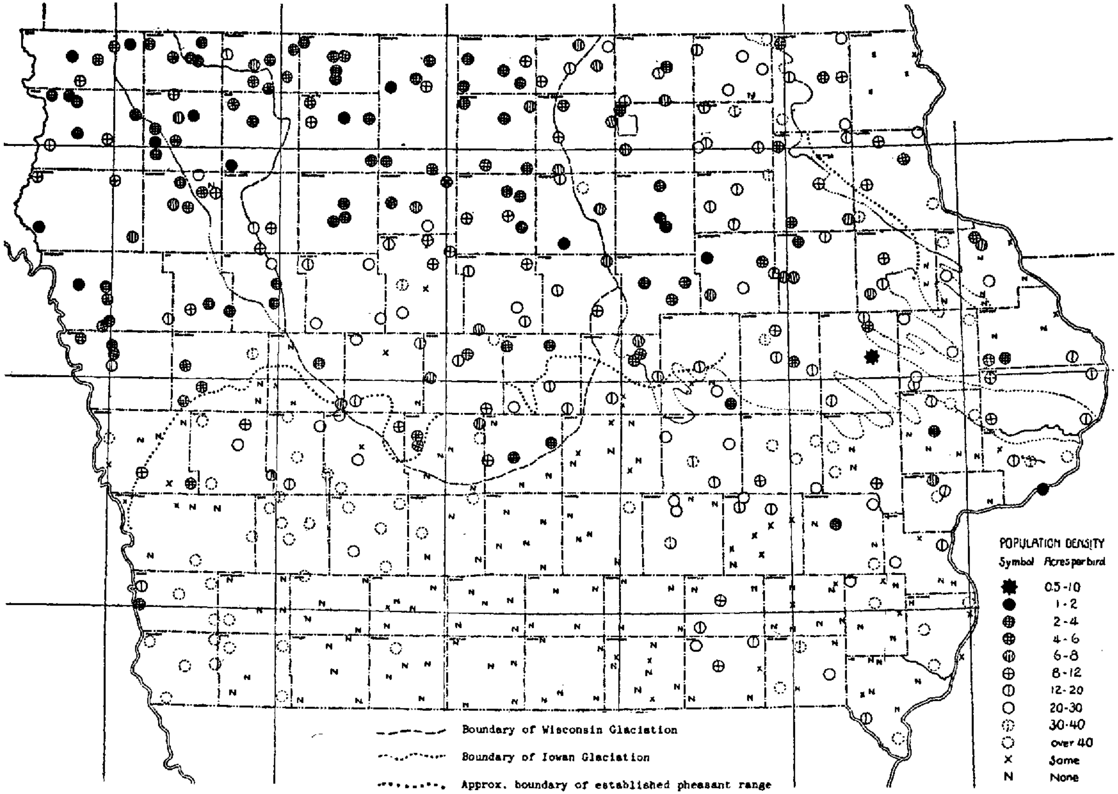
Oscar Johnson, state game warden of South Dakota, used the sample plot method for obtaining a rough spring census of pheasants. He counted the number seen during the morning and evening feeding hours on a series of representative forties. The counts were made in spring when cover was at a minimum. Each forty was counted for 2–3 successive days, preferably including both morning and evening, and the average count assumed to constitute the population. Sixteen forties (640 acres) in Spink and Beedle counties tallied an average of 2.6 acres per bird. Fifteen forties in Hanson, Davison, and Sanburn counties tallied an average of 6.0 acres per bird. The tallies were not made until the middle of May, by which time some hens were incubating. This doubtless distorted the sex ratio, which is accordingly omitted, and also unduly reduced the visible hens. If, however, we assume that the cock count is correct, and apply the true sex ratio obtained by winter trapping (see Table 13, Chapter IV) to the cocks tallied in Spink and Beedle counties, it results in a census figure of 1.8 acres per breeding pheasant.

Let the reader grasp this point: Johnson's wardens may or may not have seen all the pheasants resident on these sample forties, but what they saw is nevertheless an index to comparative abundance.

In all census by sample, the usual difficulty is not in enumerating the game on the samples, but in determining to what extent the samples are representative of the area as a whole. As already pointed out for Fig. 12, a purely geometric symmetry in

FIG. 13

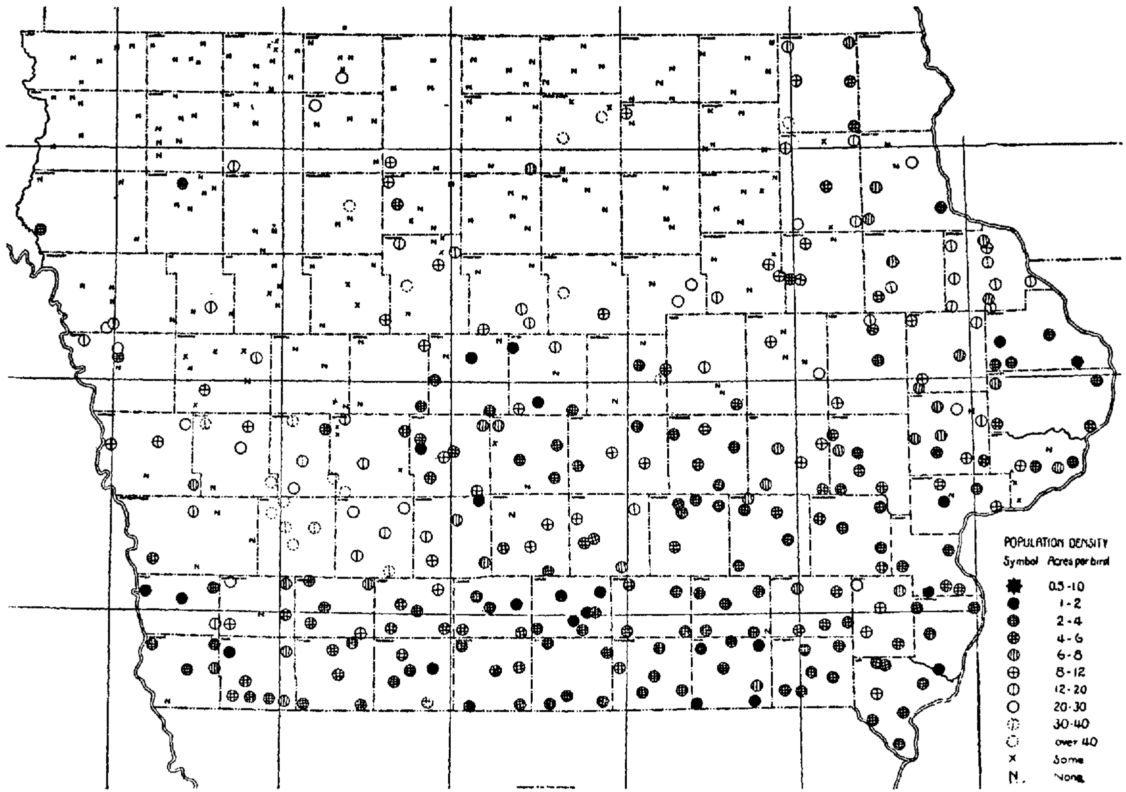
PHEASANT CENSUS OF IOWA. WINTER OF 1931–32 MADE BY THE DISTRICT GAME WARDENS AND ALDO LEOPOLD FOR THE IOWA CONSERVATION PLAN



Outline map, courtesy of Rand McNally.

Fig. 14

QUAIL CENSUS OF IOWA. WINTER OF 1931–32 MADE BY THE DISTRICT GAME WARDENS AND ALDO LEOPOLD FOR THE IOWA CONSERVATION PLAN



Outline map, courtesy of Rand McNally.

the location of the samples would be one way to get a true assortment, but this requires a huge number of samples in order to complete a census of a large area like a state.

In the Game Survey of Iowa, made during the winter of 1931–32, the services of the local wardens were available for taking a large number of samples. The condition of the roads made a geometric placement out of the question, many whole townships being impossible to enter with a car. As a substitute for geometric placement, the wardens were asked to select and census five farms in each county, if possible well scattered geographically, and in any event representing good, average, and poor densities for the principal local game bird.

Figs. 13 and 14 show the densities determined for pheasants and quail respectively.

The pheasant counts were made by "driving" one farm in each county with a crew of volunteers walking abreast through the corn or coverts. Estimates of selected farmers, checked against the drive, were accepted for the other four samples in each county.

The quail counts were made by working one farm in each county with a bird dog, or after a tracking snow, and determining the number of coveys. Coveys were converted to birds either by adding the actual number of birds seen in each or, failing that, by arbitrarily assuming 15 birds per covey. Four other farms were then censused by farmer-estimate.

A similar census of Hungarians in the northwestern counties was made, but is not here shown. The densities were similar to those of pheasant.

The maps are believed to portray quite accurately the game on the samples, but it is certain that the samples are not representative of the state or the county, in spite of the best efforts of the wardens to make them so. They portray a more favorable range of densities than actually exists. This distortion is much greater for quail than for pheasants, because of the greater continuity of the pheasant range, and the lesser proportion of *totally blank areas*.

There is another distortion arising from the fact that the northern samples were selected to show the assortment of densities for pheasant, which selections usually failed to show that for quail. Conversely the southern samples even when correctly representing the assortment of densities for quail, do not show that for pheasants. Quail are "penalized" in the pheasant country, and vice versa.

These conclusions may be drawn: In taking census samples on a game range embracing blanks, a type map is needed in order to exclude the blanks, and separate sets of samples are needed for each species of differing habitat.

This assumes that a correct total population figure is desired. As a matter of fact no such figure was needed in this case. The main objective was to show the range of densities *within the inhabited range* for comparison with other states and with future remeasurements. For these purposes the maps suffice.

The quail census was accompanied by a measurement of the rate of shrinkage in habitable range. The results are referred to in Chapter XV.

Contrary to expectation, many of the Iowa wardens quickly developed skill and enthusiasm in executing the counts. Next year's census can capitalize this skill, and the yearly repetition of the job will furnish what no state has ever had: a localized quantitative measurement of the trend of its resident game resources.

Brood Counts on Sample Strips or Areas. In birds such as ruffed grouse the brooding hen clucks and feigns to be wounded, or otherwise deliberately atrracts attention when closely approached. A rough census of adult breeding population may be made in such birds (provided the sex ratio be known or the number of males has been determined by drumming log counts) by counting the number of feigning hens encountered on sample strips of known length and width, or on sample plots of known area. The number of feigning hens constitutes an index to the number of broods, even though the broods themselves be not seen. The method is applicable only for a week or two after hatching, and only where the bulk of the broods hatch almost simultaneously. King (unpublished) developed this method in northeast Minnesota, where in 1931 nearly all the ruffed grouse broods hatched during the week of June 10 (the week when the pink ladyslippers began blooming, when the large-toothed aspen leaves were half out, and black ash buds just bursting).

The mobility of newly hatched broods appears to be very low, so there is little danger that strips run arbitrarily at right angles to the topography (such as on 40 lines) will fail to represent a true sample, or will encounter the same brood twice. The mother grouse can apparently be depended on to advertise her presence, at least up to the time when the young begin to fly, but *the distance at which* she will do so may vary according to the weather and cover. The width of the "effective strip" will vary from day to day, and is the observed average distance at which the hens are flushed on that particular day. In rain the width may approach zero. Disturbance of the brood during rain may endanger its welfare, and should be avoided in any event. Cocks are, of course, not counted in the hen tally. They may be distinguished by the greater distance flown and by their failure to feign wounded behavior.

For example: All the four north-and-south forty lines in a section are cruised on foot during a single day, during which three feigning hens and six non-feigning cocks are flushed. The average flushing distance for the hens is determined, by tally, to have been half a chain (33 feet) on either side of the line of travel. A forty is 20 chains wide, hence the sample represented by the strips constitutes $\frac{1}{20}$ of the total area. If the sex ratio is known to be 50 : 50, the census is calculated as follows:

3 = feigning hens (apparently with brood) flushed on a sample representing $\frac{1}{20}$ of the section.
60 = 20 × 3, total probable number of hens with brood.
60 = number of cocks under a 50:50 sex ratio.
120 = 60 + 60, number of grouse on section (640 acres).
5 + = 640 ÷ 120, acres per breeding grouse.
10.7 = 640 ÷ 60, acres per brood.

The weakness of this method is that it assumes that all the hens actually mate and hatch a brood, and that the brood remains alive until the count is made. As to mating, the truth of this assumption is still untested, but as to reaching the point of hatching, King found nest mortality in 1931 to be nearly zero in this species—a decided exception to the usual rule. Juvenile mortality is, of course, high, especially under unfavorable weather conditions. The largest source of error is in estimating the effective width of the strip. Under conditions of bad weather during or previous to the count, very low densities, doubtful sex ratio, or large spread of hatching dates, the method is not recommended.

Where these conditions do not interfere, however, this method may prove valuable in censusing species which yield to few of the ordinary methods of game census. The ruffed grouse is conspicuously difficult to census by ordinary methods.

Census from "Clean-ups." Effect of Influx. When something approaching a "clean-up" is made on any animal within a limited area, the known number removed constitutes the basis for a census, provided an estimate can be made of the residual population, and of the influx during the process of removal.

The probable population of other similar areas can then often be inferred by comparison.

Sometimes the "clean-up" is virtually complete, thus obviating the necessity for estimating residual population. For instance, the removal of 22,362 deer from the hoof-and-mouth disease control area on the Stanislaus National Forest in California in 1921–23 was judged by local foresters to be nearly complete. The cleaned area covered about 1142 square miles. The influx is unknown, but it had three years to take place, and in all probability was greater than the residual population. (The area filled up quite rapidly after the disease had been stamped out and the killing ceased.) The true census was, on this assumption, somewhat less than 22,362 deer on 1142 square miles, or somewhat less than 20 deer per square mile. This is probably the most accurate deer census figure for a large area so far available in America.

Sometimes tracks in the snow make possible an accurate estimate of the residual population. Thus in 1928 and 1929, 30 foxes were removed from a 14,000-acre refuge in Dent County, Missouri. Subsequent tracks showed that about three-quarters had been removed, indicating a total population of 40 foxes including residue, but without allowance for influx. Influx was impossible to estimate accurately. If it was 10 per cent, the true census would have been 36 foxes or 1 per 400 acres. Since the clean-up extended over two winters, it might, however, have been 50 per cent, which would change the true census to 20, or 1 per 700 acres. The longer the time, the heavier the population pressure outside, and the greater the mobility of the species, the harder it is to estimate influx.

If a clean-up occurs on an island (either a physical island, or an ecological one surrounded by non-habitable range for the species in question), then the error due to influx is ruled out, and the only remaining source of error is the estimate of the residue.

Even a very refractory species can be thus censused on "islands" if it can be trapped. Thus the Pennsylvania Game Commission in 1930 trapped 122 cottontails for restocking purposes on Barbadoes Island (49 acres) in the Delaware River opposite Norristown. This island is isolated for rabbits, although pheasants fly back and forth. There had been no hunting. The removal was 122 rabbits ÷ 49 acres = 2.5 rabbits per acre. Wardens estimated 50 rabbits left, which makes the probable population (122 + 50) ÷ 49 = 3.5 per acre.

A partially complete census of the "clean-up" type sometimes resulted from the "deer drives" of pioneer days. A drive in Medina County, Ohio, in 1808 (*Game Survey*, p. 194) netted 300 deer killed from 25 square miles, or 12 per square mile. Probably by no means all the deer were killed. Another census estimate, doubtless based on drive data, was made by Noah Major in 1820. He estimated there were 20,000 deer in Morgan County, Indiana, or 53 per square mile.

These "clean-ups" by driving, being made in one day, are free from the influx error which attends the slower processes of trapping or piecemeal shooting.

The rabbit drives still held in the western states yield a census of the "clean-up" type. Thus a drive covering 8 square miles held at Roberts, Idaho, in the winter of 1924–25, yielded 5000 jackrabbits, or about 1 per acre. The leakage is reported by L. L. Laythe of the U. S. Biological Survey as having been less than 5 per cent. During the next year rabbits were at the peak of their cycle, and several smaller drives covering about a square mile each yielded 2–4 jackrabbits per acre. The year after there were no rabbits.

Table 15 summarizes the result of these drives, and four others in Arizona reported by D. A. Gilchrist of the Biological Survey.

The Lincoln Index; Census by Banding Ratios. Lincoln (1930) suggests the use of banding returns as an index wherewith to census that most difficult group, the water-fowl, for the whole continent. This concept, which we may call the Lincoln Index, is one of the most important intellectual contributions so far made to the art of game management.

TABLE 15

CENSUS FROM JACKRABBIT DRIVES

Date	Locality	Area Driven	Number Killed	Acres per Jackrabbit Killed	Estimated Leakage	Probable Acres per Jackrabbit
1924-25	Roberts, Idaho	5,000	5,000	1.0	5%	0.9
1925-26	" "	600	?	?	?	0.2-0.5
April, 1925	St. Johns, Ariz.	5,100	2,525	2.0	10%	1.8
June, 1927	Artesia, N.M.	640	156	4.1	2%	4.0
May, 1923	Tucson, Ariz.	1,280	300	4.3	5%	4.0
Nov., 1920	Avondale, Ariz.	2,560	1,200	2.1	2%	2.1

Lincoln observed that of the total number of ducks banded at a given station, the percentage of bands returned after being killed by hunters, the first season after such banding, is surprisingly constant from year to year, and appears to average around 12 per cent.

The percentage of banded ducks killed is presumably the same as the percentage of non-banded, *i. e.*, the continental population.

If, therefore, the licensed hunters would turn in a complete record of their annual bag, an annual continental census could be computed as follows:

$$\text{kill} = 12 \text{ per cent of the population}$$

$$\text{population} = \text{kill} \times \frac{100}{12}$$

The unknown crippling loss is the same in banded and unbanded birds, and hence cancels out. Some banded ducks are killed but not reported. These would introduce an error, and so would the unreported kill of unbanded ducks, but these two errors would tend to offset each other.

Assuming a kill of 5,000,000 ducks, Lincoln calculates (as a sample) a fall population of 42,000,000 ducks.

Lincoln's principle of applying the banded kill ratio to the unbanded population will work wherever large numbers of wild stock can be banded throughout the area to be censused, and where the total kill as well as the banded kill can be determined. It is the same principle which Stoddard used to determine the survival of Mexican versus native quail. It yields a kill ratio, but usually not a species ratio even if the records are itemized by species, since the various species are seldom either trapped or killed with equal facility. Density can be computed from such a banding census wherever a clean-cut area is covered.

The practical application of the Lincoln index to a continental duck census is for the moment hindered by the lack of: (1) the unreported bands killed; (2) the unreported unbanded kill. To get some light on the first unknown, I asked a number of game officials and game managers to estimate the percentage of bands killed but not reported in their respective jurisdictions. The estimates are: Carolinas, 80 per cent; Connecticut, 50 per cent; Memphis area (clubs) 5 per cent, (elsewhere), 10 per cent; Arkansas, 60 per cent.

Indices to Abundance. Where it is impracticable to use direct total or partial enumeration, or "clean-ups" on sample areas, or banding ratios, it is often possible to accomplish the purpose in hand by the skillful use of "indices." An index to a game population is any condition which can be measured, and which may be expected to vary in proportion to the population which cannot be measured. The index is used to measure the population indirectly. Indices usually yield only relative abundance but sometimes absolute abundance.

Scotch gamekeepers, for instance, obtain an absolute census of grouse nests (*i. e.*, breeding pairs, since the red grouse is monogamous) by counting the groups of "clocker droppings" along the burns (rivulets). The "clocker" form of dropping is peculiar to incubating hens. Each hen is said to water at a fixed point whenever she leaves her nest to feed, and there deposits the "clocker." The number of groups of clockers along a stream therefore constitutes an index to the adjacent population of incubating hens. If there is some correspondingly fixed place of deposit, this ingenious method of census might be found applicable to some of the American grouse. Ruffed grouse, at least, do not deposit the clocker at any fixed place.

Direct count of the nests on a known area yields, in monogamous species like red grouse, a spring census, and in polygamous ones an index to abundance which is virtually a census. However, before accepting such a sample as representative of a large area, it should be ascertained whether there has not been any concentration of nesting activities which would make the counted area unrepresentative.

Thus one observer (*Du Pont Conservation News*, 4/3/31) reports 15 turkey nests "within a radius of half a mile" in Winston County, Alabama. Taken literally, this means 500 acres, or 1 nest per 33 acres. A covey count on 100 square miles of (presumably) similar surrounding range yielded (after the broods had come off) 50 flocks averaging 11 each, or 1 brood per 1300 acres. There is at least an indication here that the nesting was concentrated on the area in which nests were counted. This is merely offered as an example of the possible error inherent in all census work where small areas are relied upon to sample population density.

Dice (1930 and 1931*b*) suggests the number of individuals seen per hour in various habitats as an index to relative abundance of two or more species. Nocturnal or flocking birds could not, of course, be so measured. He cites Linsdale as using birds per day, expressed as frequency curves, and Raunkiaer as using the frequency with which various species occurred in a fixed system of sample plots. All of these ideas yield indices to relative abundance, rather than a census.

Taylor (1930) obtained the relative abundance of various rodents by tallying the number seen per hour in visible species like prairie dogs. In nocturnal rodents he used the percentage of traps catching a rodent, after being set for one night. He also used the carcasses found at poison bait spots exposed for one night, the burrows counted per acre, and the fecal pellets counted within a wire hoop set down at fixed intervals. Some of these ideas may be applicable to game census. The last one especially ought to be applicable to deer and rabbits, which deposit durable pellets at random over the range.

Taylor and Vorhies (unpublished) are now using a unique index which yields a direct census of visible diurnal rodents on fenced cattle ranges in Arizona. They compare the number seen with the number of cattle seen, and then compare the ratio with the known number of cattle. For example: within a fenced pasture they count the number of jackrabbits seen for each cow seen within a strip of paced length, the width of which is the apparent "flushing distance" of the jackrabbits. The total number of jackrabbits can be calculated by applying the tallied ratio. The proportion would be:

Cattle on range:	cattle tallied =	jackrabbits on range:	jackrabbits tallied
(known)	(known)	(unknown)	(known)

Only Westerners inoculated with a tincture of that indefinable body of skill called "cowsense" appreciate where the cattle come in. Why not tally the rabbits direct? Because this is a brush range, on which a certain proportion of both jacks and cattle escape observation, within the counted strip, by standing motionless, or by beating a retreat in line with a screen of brush. The method assumes that the same percentage of both cattle and rabbits thus eludes the click of the tally-register.

Leopold (*Game Survey*) tried "coveys per dog per day" as an index to the abundance of quail in various regions, but found it unsatisfactory because of the varying ability of dogs and the varying nature of coverts. With the same dog on the same ground, however, it would probably be a good index wherewith to compare one year with another.

Flushing Rates. Many of the indices to abundance developed by zoologists are premised on intensive observations by a few men, rather than mass data obtained from many untrained observers. The game manager has available in the hunter a source of mass data as yet largely unexploited.

The Iowa Game Survey (1932) used the number of pheasants flushed per man-hour by selected parties of hunters as an index to density, and later compared the results with the sample-plot census already described. The two checked very well in indicating the geographic distribution of density. The flushing rates for the counties open in 1931 are shown in Fig. 15.

Flushing-rate is an accurate index to abundance only where the localities being compared are similar in cover or escape facilities, and where the hunting is done in the same way at the same time. Iowa pheasant hunting satisfies these criteria almost perfectly. The hunting is all done in standing corn, there is little other cover, the hunting is all compressed into two days, and the method of "walking in line" is nearly universal. Varying skill in choosing territory, varying use of dogs, varying hours of the day, varying weather, etc., are all either matched out by the extraordinary uniformity of the set-up or can be obviated by the mass of data that is obtainable. The only troublesome variable is the care with which various parties keep count, and even these errors probably tend to compensate. It was necessary, of course, to use the party rather than the individual as the unit, and to have one individual in each party responsible for keeping track of the birds flushed at the end of each "drive."

Collections of Census Data. One of the largest collections of rough census and kill figures so far available is that made by Adams (1926). It deals largely with mammals, fur-bearers, and fish, whereas my publications emphasize birds. Good mammalian census figures are also offered by Seton (1929).

OTHER MEASUREMENTS

Measuring Trends by Bag Records. The Lincoln banding index derives from the bag record of a single year an actual enumeration or census. Bag records through a term of years may likewise be used, without any enumeration, as an index to the *trend* of a population, provided the hunting is done on the same ground by the same method by a single individual at regular intervals throughout the season (or by a large number of individuals so that variations in individual proficiency and seasonal game habits cancel out).

Records of game seen, as well as of game killed, are usable for the same purpose under the same conditions.

Thus Leopold (1930) records jacksnipe seen and killed in Dane County, Wisconsin, during weekly hunts from 1919 to 1929, by himself and A. W. Schorger (see Fig. 16). Three of the four graphs (*A*, *C*, and *D*) show a strong downward trend, including the two most dependable ones (*C* and *D*) in which the birds seen and killed per trip are reduced to a uniform time-interval (per full day of 8 hours). The conclusion was that a decrease of perhaps 50 per cent has taken place during the period measured.

A similar record by Leopold (1925) is shown in Fig. 16. This compares ducks seen per year, and ducks seen and killed per day, in the middle Rio Grande Valley, New Mexico, during weekly hunts from 1918 to 1923. Graph *B* is considered more de-

Fig. 15

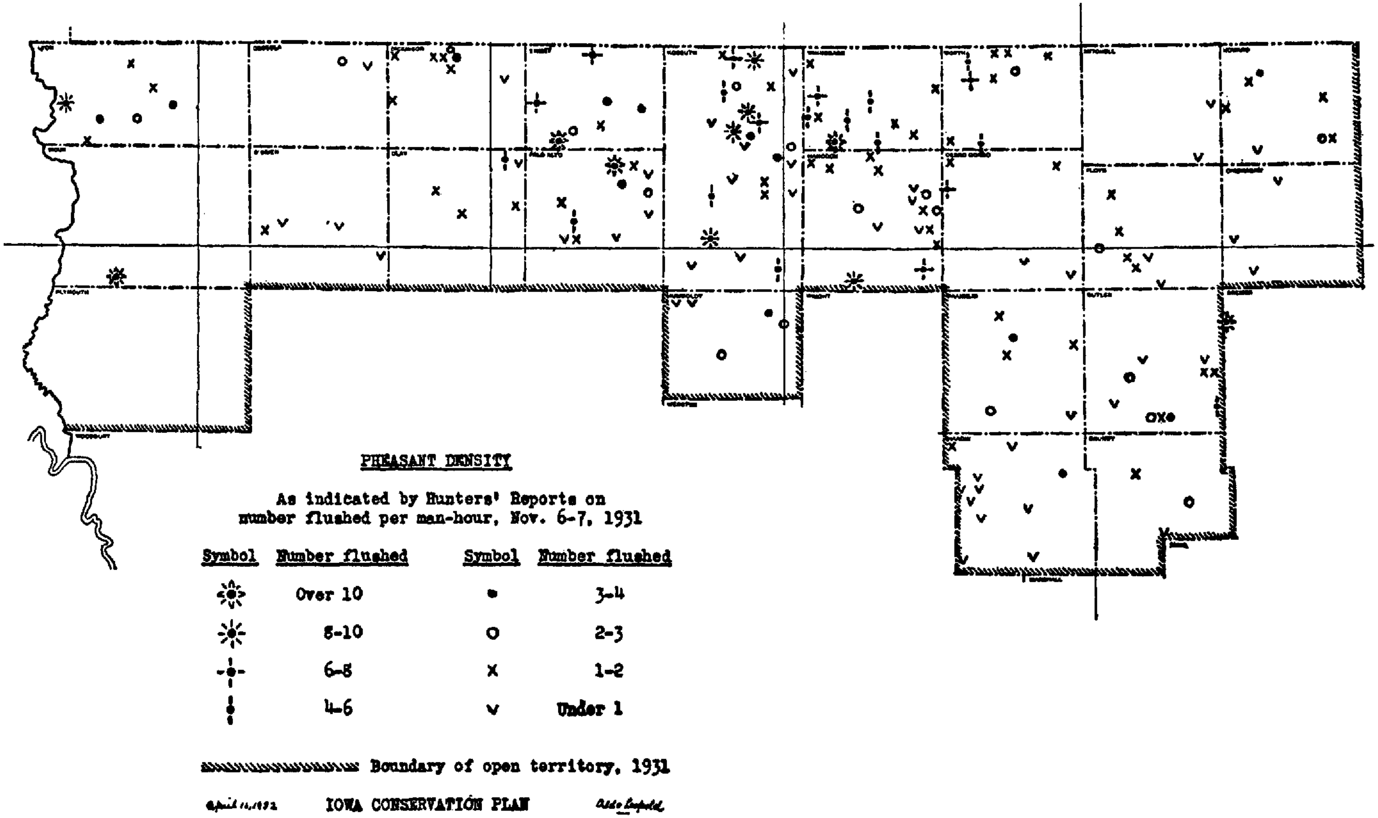
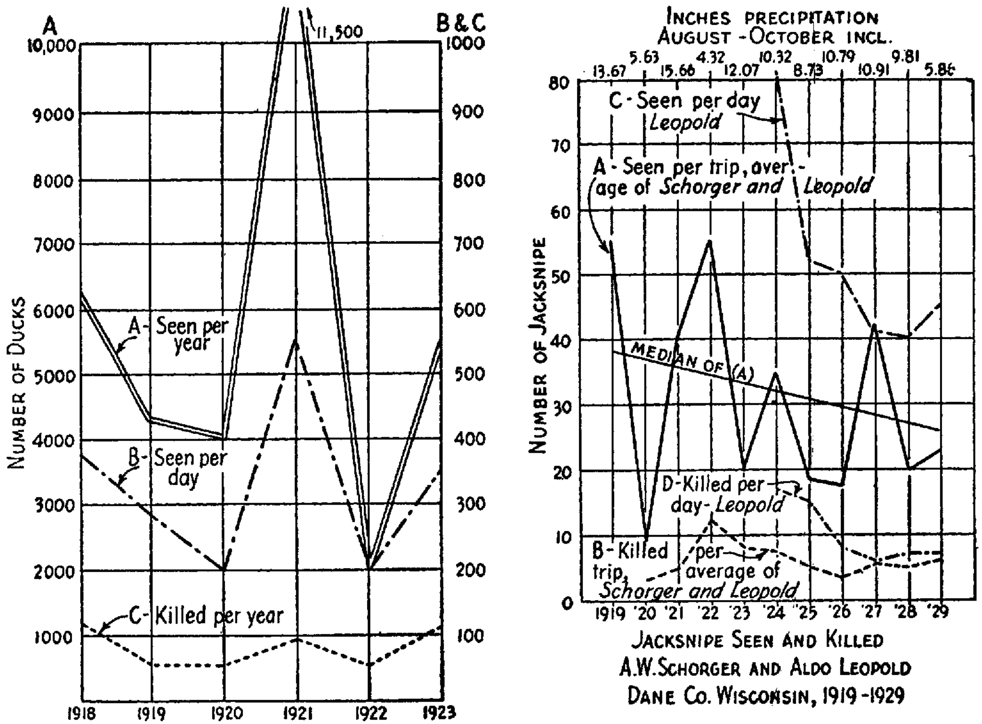

PHEASANT DENSITY
As indicated by Hunters' Reports on
number flushed per man-hour, Nov. 6-7, 1931
Symbol Number flushed
Over 10
8-10
6-8
4-6
Symbol Number flushed
3-4
2-3
1-2
Under 1
Boundary of open territory, 1931
IOWA CONSERVATION PLAN

Fig. 16

MEASURING TRENDS BY BAG RECORDS



Ducks Seen and Killed ~ Aldo Leopold
Middle Rio Grande Valley, N. Mex., 1918-23

Jacksnipe Seen and Killed
A. W. Schorger and Aldo Leopold
Dane Co. Wisconsin, 1919-1929

pendable than *A* or *C* because the ducks seen per trip are reduced to a uniform time interval (per day) thus eliminating the disturbing influence of varying numbers and lengths of trips. Neither *A*, *B*, nor *C* shows any strong upward or downward trend. The conclusion was that the increase in ducks currently purported to have taken place in the country at large during that period had *not* taken place in the Rio Grande Valley.

Bag records from large numbers of individuals (such as shooting club journals or licensees' returns of game killed) are useful indicators of trends in game abundance, provided no great change has taken place in number of hunters or hunting methods and equipments. When such variables have entered for a short term of years they are hard to allow for. If, however, a kill is sustained through a long period in spite of such variables, the record becomes very valuable as an indicator of productivity. Such records are covered in the next chapter.

The *measurement of fluctuation* is, of course, the measurement of trend in game population through a long period of time. Section *D* of Fig. 7 shows how bag records on Scotch grouse moors were used by Leopold and Ball (1931*b*) to measure fluctuation through a long period. Curve *B*-3, Section *B*, shows Seton's use of sales of rabbit skins (practically a bag record) for the same purpose. Short-cut methods for measuring past fluctuation are suggested under the discussion of cycles in Chapter III.

Measurements by Trapping and Banding. By far the most important development to date in the art of measuring game is the technique of bird banding, suggested by Cole (1922) in 1901, and now widely used the world over.

Game birds are usually harder to trap than songbirds, and the young are not born helpless, seldom return to the nest, and hence cannot be banded in the nest. For these reasons students of game birds have been somewhat slower to take advantage of this technique than other ornithologists, but the practice is growing rapidly, and its possibilities have as yet scarcely been touched.

The proper function of this volume is not to attempt a description of banding technique in detail (this is adequately done in the *Manual for Bird Banders*, Lincoln and Baldwin, 1929), but rather to point out the utility of this technique in the quantitative solution of game management problems.

It is already apparent that banding constitutes the best and only method for measuring the mobility of game populations, and for determining the migration routes of migratory species. It is also one of the best methods for determining the sex and age composition of game populations. It can doubtless be used for many other measurements, provided the species can be trapped, caught on the nest, or otherwise captured for the purpose of affixing the band, and provided the species is shot as game, or is otherwise susceptible of recapture, for determination of its subsequent movements.

The classical example of the use of banding for determining the mobility and composition of an upland game stand is Stoddard's *Georgia Quail Investigation* (1931, p. 167). By trapping large quantities of quail he first of all determined the sex ratio during the early spring season to be about 55 males : 45 females. By comparing this ratio with a sex count of hunters' bags (53 : 47) on the same territory during the immediately preceding shooting season, he found that either (1) the male is slightly less likely to be killed by enemies or shot by hunters than the female, or (2) there is a progressive differential mortality working against the female. By banding the quail as trapped, and noting the kill of banded birds during the next and also succeeding shooting seasons, he determined the annual mobility of the individual bird (see Table 4). By banding like numbers of Mexican quail planted on similar range and comparing their percentage of recapture during subsequent shooting seasons, he determined the superior survival of the native bird.

The variety of management problems, the solution of which lies in banding, is exemplified by Austin's (1929) discovery, through banding, that terns do not breed until their second season. He banded a large number of young terns on the Cape Cod Rookeries just before they were able to fly, and during the next year found that these particular birds did not reappear as breeding adults. An examination of bands recovered in the country at large, however, revealed the fact that during their first year they were scattered over the continent, but not on breeding rookeries. During the second year, however, they reappeared as breeding adults on the original rookery. The paucity of existing information on minimum breeding age of game species is clear from Table 1, and its importance is shown by a comparison of the unimpeded increase curves in Fig. 3. The obvious conclusion is that the new banding technique should be used to establish the breeding age of species now in doubt, such as woodcock and jacksnipe.

One of the present needs of game management is the development of banding techniques for mammals. Experience with birds proves that it is only by this means that the life history facts requisite for intelligent management can be obtained.

Substitutes for Banding. The basic purpose of banding is, of course, to make possible the identification of individual animals. Occasionally individuals can be identified without banding. Thus Leopold (*Game Survey*, p. 229) reports a domestic cat treed by coon hunters four miles from the farmhouse where the cat, on being identified by its markings and behavior, was known to live. Accordingly we know that the daily cruising radius of this predator may be as high as four miles.

Important light has been shed on the breeding habits of pheasants and quail by observing the behavior of one-legged, lame, white-spotted, or otherwise identifiable individuals through a period of time.

One of the questions usually considered as answerable only by banding is the degree to which individual birds shift from one covey to another. Under some circumstances, however, a fairly reliable answer can be obtained without banding. Thus Yeatter (unpublished) made repeated covey counts on all of the Hungarian partridges within an area of several square miles in Lenawee County, Michigan, during the winter of 1930–31. The count of each covey throughout the winter period either remained stationary or showed a slight and gradual loss. None of the coveys showed a single gain. The covey locations remained constant, and the covey ranges seldom overlapped. This behavior constitutes at least strong circumstantial evidence that no trading of individuals from one covey to another was taking place during the winter season, and to this extent constitutes a substitute for banding. Errington (1930, 1931) applied the same method to quail.

Such circumstantial conclusions should, of course, be checked up by actual banding, but since this costs much time and effort, the temporary substitute is distinctly useful to the game manager.

Enough has been said to make it apparent that the three basic techniques (counts, indices, and marks or bands, and doubtless others yet awaiting discovery) may be combined in many ways to enumerate game or measure its habits or condition. The particular combination to use for any given local problem must be left to the ingenuity of the investigator. The next chapter will show how the same techniques may be used to measure the productivity of a population. Productivity measurements frequently yield information on census or the other subjects covered in this chapter. The whole subject of range, population, and productivity is in fact one integral whole, here arbitrarily divided merely for convenience in presentation.

Phenological Tables. Measurements of game phenomena (such as hatching dates, for example) are sometimes so difficult to secure that several years' observations must accumulate before there are enough data to justify a conclusion. If in compiling the data the several years be arbitrarily lumped by calendar dates, an error may be introduced because certain years were abnormally late or early in their weather, and hence in the seasonal progression of their phenomena.

Game dates for such abnormal seasons may be adjusted to normal if the observer has taken the precaution to keep a cumulative record of the dates of typical seasonal phenomena. Such a record is called a phenological table. Dates of first leafing, flowering, fruiting, sex-calls, pairing, egg-laying, hatching, etc., are good items for such a table. Dates of bearing young in mammals are poor, because they are influenced by the weather preceding gestation. Dates of arrival of migrants are poor, because they are influenced by the weather at the point of departure as well as at the point of arrival (Main, 1932), and by the length of daylight, which is entirely independent of local weather (Rowan, 1931).

To illustrate: If lilacs usually first bloom on April 15, but during a particular year do not bloom until May 1, the indication is that the season is two weeks late. The game dates may be "slipped back" to normal in adding the data for the late year to the data for other normal years. This example assumes that the game phenomenon in question is wholly determined by local weather. As indicated above, such assumptions should be made with caution.

Determining Age. All measurements of either game population or game productivity are enhanced in their significance and value if the sex and age as well as the number of individuals be determined.

How to determine sex or age by the ordinary aspects of plumage or pelage is often obvious, and is usually fully covered in standard works on natural history and anatomy.

How to determine age by other criteria is less often mentioned.

Stoddard (pp. 70, 82) found that the outer two primaries in the juvenile bobwhite plumage are sharper-pointed and narrower than in the adult, and develop so late in the chicks during their first season that they are not replaced until the moult of the second fall, before the hunting season. Hence they offer a convenient mark by which to classify the bag into birds of the year and birds one and one-half years and older, and to classify breeders into one-year-old birds and older.

Whether Stoddard's criterion holds for our other quails is not known.

The *Grouse Report* (p. 64) offers a somewhat similar criterion for red grouse. Birds of the year, during the hunting season (September) have the same narrow-pointed primaries as in quail, but in addition the third primary is short and often shows a "blood-quill" at its base.

Whether this holds for American grouse is not known.

The *Grouse Report* (p. 66) also suggests the softness of the skull and the strength of the jaw as criteria:

> "The weight of the bird is allowed to hang without support by holding the tip of the lower bill only. The bone of an old bird's jaw easily stands this test, but the soft jaw of a young bird of three or four months cannot carry its weight, and the jaw either bends or breaks."

Determining the age of chicks and juvenile birds is discussed in Chapter XV under "Nesting Studies."

Lovejoy (*Michigan Biennial Report*, 1929–30, p. 257) and Cahalane (1930, 1931) investigated methods for telling age in deer:

> "No direct relationship was found between the number of antler points and age. Up to about four years the number of points quite certainly tends to increase, but after four years the number of points remains fairly constant for an indefinite period, and in very old animals may actually decrease.

"It was found that age could be determined directly from the teeth up to the fifth year, after which the precise age of individual heads could not be determined directly."

Cahalane compared dentition with diameter of antler beam, and diameter of antler burr, in a series of 260 skulls. He found the beam diameter, 2 inches above the burr, to increase quite consistently with age, and offers the following table for classifying large series of antlers into age classes:

TABLE 16

AGE CLASSES OF MICHIGAN WHITETAIL BUCKS BY ANTLER DIAMETER CLASSES

(Reproduced by permission of *Journal of Mammalogy*)

Diameter of Antler Beam, millimeters	Age, years
Up to 19	1½
20–22	Divide equally between 1½ and 2½
23–27	2½
28–34	3½ – 4½
35–37	One-third are 3½ – 4½ Two-thirds are 5½
38+	5½+

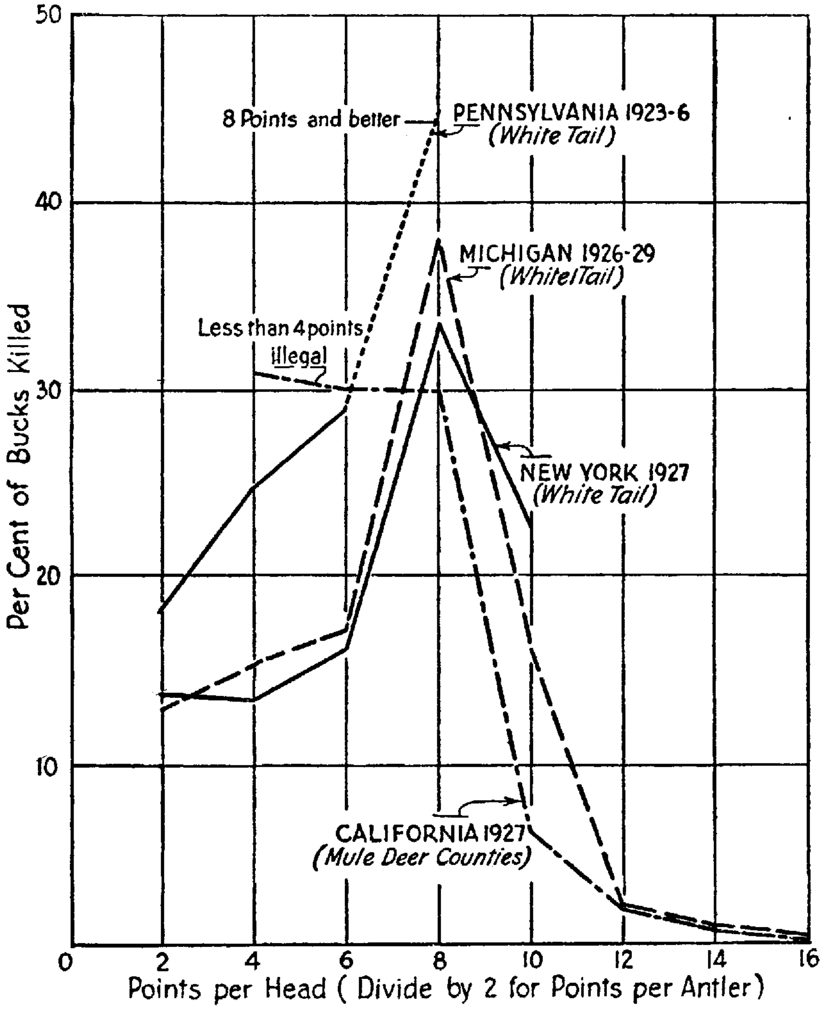
This table might not apply to other states, and would, of course, not apply to other species, although the principle of using antler-beam as an index to age probably would.

In the management of deer, the general range of antler point classes in the kill of various states and species is always of interest, and may be of value. Fig. 17 gives the frequency of heads of various sizes in four states. The Michigan curve is Cahalane's. The other curves are taken from data in official reports.

Eight-point heads are evidently the most frequent in all the states, but the various states differ somewhat in the representation of prime 10 and 12 point heads, and immature 2 and 4

FIG. 17

FREQUENCY OF ANTLER CLASSES IN ANNUAL KILL



pointers. Pennsylvania and California seem to have killed a high percentage of young bucks. Unfortunately the prime Pennsylvania heads were all lumped at "8 and better," so there is no way to tell whether prime 10 and 12 pointers were unduly scarce. There is also some doubt whether the California heads were all mule deer. The official reports do not distinguish between mule deer and blacktail, so the reports for the counties in which the former prevail had to be used as the basis for the California curve.

Until better information is available, the Michigan curve may be assumed to represent the kill from a normal herd of whitetail deer. It is known that deer were holding their own or increasing during the period measured. The curve represents counts on 2000 heads.

Summary. Census is the first step in management. A census can be made by enumerating the game on sample areas, by banding ratios, or by indices.

Direct enumeration is practicable mainly with population units which are either isolated, or moving along a fixed route, or very sedentary.

In comparing densities from censuses, the blanks in large areas invalidate direct comparison with small ones.

Invisible animals can be directly enumerated in snow, or by scenting dogs, or when forced into the open, or when "cleaned-up" on a given unit. Influx is a source of error in "clean-up" samples.

In censusing a large area, it is harder to select representative samples than to count the game thereon. Samples taken arbitrarily along fixed land-lines or in a geometrical pattern have the best assurance of being true samples, but they must be numerous.

Banding ratios yield a census when the population is the only unknown in a proportion. The three knowns are determined by banding. It is, in effect, a method of using samples in time instead of in space. Migratory game yields only to this method.

Indices yield a census when the index condition, which is subject to measurement, varies with the population which is not.

Either indices or samples can be used to determine population trends in time.

Counting the invisible hosts of migratory waterfowl over a whole continent by means of such an ingenious device as Lincoln's banding ratio is a feat which has excited either incredulity or admiration, depending on the mental capacity of onlooker. Even those able to grasp the method, however, have often not yet grasped the fact that "finding out how many there are left" is the least of the purposes of game census. Measuring the response of game populations to changes—deliberate or accidental—in their environment is the big purpose. Continuous census is the yardstick of success or failure in conservation.

Chapter VII

MEASUREMENT AND DIAGNOSIS OF PRODUCTIVITY

MEASUREMENT

Definitions. Productivity has been defined as the rate at which breeding stock produces a removable crop or additional breeding stock.

If the crop is not to be removed its measurement is accomplished, as in forestry, by comparing the annual increment with the original stock. The unit of measurement is the ratio or per cent of increase per year.

If the crop is to be removed by hunting, its measurement is accomplished, as in finance, by comparing the interest with the capital, or as in farming, by comparing the yield with the seed. The unit of productivity, where the increase is removed, is the ratio or per cent which can be removed yearly without diminishing the capital. This we may call the kill-ratio.

Often, of course, only a part of the crop is removed as kill, the rest being left as capital accretion. This is the proper policy where a larger breeding stock is desired.

On fully stocked ranges, however, where the population is to be kept stable, all of the annual increment can be removed by hunting except that part removed by other factors. This is the normal case, and unless otherwise specified, will be assumed as a premise in the following discussions. In such normal case, productivity is synonymous with the annual yield. The word "yield" being shorter, it is often used in preference.

Sometimes the breeding stock cannot be enumerated. In such cases a rough measure of productivity is obtainable by comparing the kill with the area which produced it, instead of with the breeding stock which produced it. Such a ratio we may call an area-kill.

If a covey of 10 quail, for instance, represents the breeding stock on 40 acres of range, and formed 5 pairs producing 14 eggs each resulting in 5 grown young each, the increase would be 25, or 250 per cent. If 15 were removed by hunting (and 10 later by other factors), the kill-ratio would be $15 \div (10 + 25)$ or 43 per cent. By the next breeding season there would still be 10 birds left to increase and sustain a similar kill.

If the number of breeding stock were not known and not ascertainable, but nevertheless if 15 birds were killed year after year from the 40 acres in question, the area-kill would be one bird per 2.6 acres, and this would furnish a rough measure of productivity.

It may be remarked in passing that the phenomena of productivity in fish are now being expressed in terms of poundage, rather than number of individuals taken, per acre. Thus Adams (1926) points out that the yield of whitefish in the Great Lakes runs up to a pound per acre per year, but in artificially fed ponds carp have yielded as high as a ton per acre. Poundage is the unit because fish vary so much in size.

Need of Standards; Chapman's Formula. A scientific basis for a yardstick of productivity is the formula devised by Chapman (1928, p. 120) which, for populations at equilibrium, is $C = \frac{B}{R}$, where C is the concentration, or census of the population unit, B is the breeding potential and R is the environmental resistance or the sum of the factors.

S. A. Graham suggests that game management could build up from this formula, or from the form $C = B - R$, an accurate yardstick for comparing all grades of productivity in all species. It is hoped that somebody will do this. That part of R over and above the kill is the true index, in that it adds up the "drag" of the factors other than hunting.

However, in actual practice, the value of C is seldom known, so it seems more practicable at this stage to seek a yardstick in comparisons of performance as expressed in ordinary terms of area, kill, and where possible, census.

Normal Productivity. Foresters use what they call a "normal" forest as a standard for measuring the condition of other forests. This conception of normalcy is believed to be a useful standard for measuring productivity in game. When a forester predicts the possible crop which he can remove from a given area of timber land, he bases his prediction on a comparison with the yield of the *best similar area he has measured.* "Similar" means having the same species, age, and site quality. From the measurement of many such optimum tracts, he builds up tables called normal yield tables.

So in game we may measure productivity by comparing the census and the kill-ratio with that of the *most productive similar range*. This means eventually setting up for each species in each region ranges which will meet this definition of normalcy, and measuring the population and kill on each. Each of these will then serve as standard with which other areas may be compared.

Measuring the Kill. Few concrete examples of measuring the kill can be given, because in this country few attempts have as yet been made to measure it.

On a private holding the method is relatively simple, consisting merely of a journal in which each hunter is required currently to enter his bag. Such journals are frequently kept by duck clubs, but in migratory birds the kill does not represent the productive capacity of the club grounds.

On lands open to public shooting, the method must usually be applicable to large areas, such as national forests, counties, or entire states. For example: On the Gila National Forest in New Mexico the "check-out system" is in use. This works best where the possible points of entrance and exit are few, and where the open season is short. There are five points of entrance and exit to the Gila, and the open season is ten days. Officers are stationed at the points of entry and exit authorized to register all cars as they enter, and check the licenses of each individual hunter. The same officers later check out each departing car, after an inspection of the bag of each hunter. In this manner the total kill of deer and turkey is quite accurately ascertained. By examining the heads and by verbal questioning at the exit point, valuable statistics are also obtained on antler classes and on sex and age classes seen by each hunter.

Michigan took advantage of the same principle of "constricted exits" to measure antler classes in her deer kill. Cahalane (1931) examined and measured all deer carcasses transported across the straits of Mackinac, and thus obtained a reliable cross-section of the kill brought out by non-residents from the Upper Peninsula.

On the state forests of Pennsylvania substantially the same system is applied to deer as on the Gila, but is executed by visiting the hunters' camps, rather than by checking at the points of entry and exit.

Some states measure the kill of big game by means of a tag system. A tag is issued with each license, and is required to be attached at all times to each head of game killed. Some kind of return report is required, by which the proportion of used tags is determined.

Other states, such as Minnesota and Wisconsin, measure the kill by a compulsory report of game killed by each licensee, no license for the ensuing year being issued if the report is not made. This penalty, however, is so far nowhere enforced.

A sample plot system could be used as a means of measuring the kill on large areas, but no such system is as yet in actual use.

In general, it should be pointed out that questionnaires, tags, and other "automatic" devices for inducing the individual hunter to report his kill are of little avail for productivity measurements unless related to a definite unit of population or range. It is usually not feasible so to relate them, unless the population unit is detached or unless the range unit comprises a whole state or some other legally recognized subdivision. Such devices are, however, useful for determining the bag per hunter, or to analyze the bag for sex, cripples, or other matters within the scope of his observations.

Illegal Kill and Crippling Loss. A true measure of the toll by hunting should take account of the illegal kill, and also lost game and disabled cripples. Unless these losses are added to the legal bag, the true yield is not determinable. The ratio of illegal to legal kill of course varies greatly as between localities and species, and its accurate measurement is exceedingly difficult. It is probably seldom less than 10 per cent of the legal kill. The Pennsylvania Game Commission estimated the illegal deer kill in that state as averaging 5 per cent during the years 1921–1925.

The crippling loss has been measured quite often for waterfowl on the basis of area (*Game Survey*, p. 208), but seldom for any kind of game on the basis of per cent of the legal kill. The crippling loss in waterfowl is higher than in any other class of game, and doubtless sometimes approaches or even exceeds the kill in magnitude. Unregulated competition or "free hunting" increases it. Approximate measurements of the cripple: kill ratio are feasible and are now being attempted on Iowa ducks.

In 1916 I sent a confidential questionnaire on cripples to a list of New Mexico deer hunters who had been carefully selected to represent various degrees of skill. Their replies indicated 10 deer believed to have been seriously crippled for 48 legal bucks brought to bag, or a 21 per cent crippling loss. This percentage is believed to be low, however, because not all of the replies seemed willing frankly to admit cripples, and modern long-range rifles undoubtedly cripple many deer without the hunter's knowledge. The crippling loss on deer in New Mexico is believed to be at least 30 per cent of the legal kill.

The following table, compiled from my hunting journal, shows the percentage of small game believed to have been crippled during five years' hunting in the Rio Grande Valley of New Mexico. During this period an extra good retriever was used at all times. Hence the percentage is probably as low as is ever attained in that region.

TABLE 17

CRIPPLING LOSS

	Doves			Ducks			Quail			Total		
Year	Killed	Lost	%	Killed	Lost	%	Killed	Lost	%	Killed	Lost	%
1919	166	20	12%	57	5	10%	20	5	15%	243	28	11%
1920	112	18	16%	58	10	17%	96	27	26%	266	55	20%
1921	86	8	9%	97	11	11%	105	8	8%	287	27	9%
1922	151	10	7%	57	4	7%	108	24	22%	316	38	12%
1923	90	4	4%	113	21	18%	26	2	8%	229	27	12%
1919-23	605	60	10%	382	51	13%	355	64	18%	1341	175	13%

The Iowa Game Survey compiled questionnaires submitted by 129 parties of pheasant hunters in 1931 dealing with crippling loss and other questions. The crippling loss in Iowa pheasants is very high, due to the heavy weedy corn in which they are hunted, to the well-known running powers of this species, and to the hectic atmosphere which inheres in gang hunting when squeezed into an excessively short season. Of 11,230 pheasants reported flushed, 2964 were bagged and 968 crippled but not bagged, an apparent cripple: kill ratio of 3 : 10. It is almost certain, however, that many parties reported as cripples only the birds knocked down but not found, omitting the many hit birds which were not downed. The real cripple-kill ratio is probably at least 6 : 10.

Kill Ratios. Statistics based on experience are the only available means of arriving at the proportion of the game population which may be safely killed on any given area without reducing the breeding stock or the size of subsequent crops. The subsequent crops are the best measure of whether the breeding stock has been unduly reduced. Consequently statistics must cover a defined area for a period of years, and should if possible be accompanied by an annual census, if a kill-ratio is to be correctly determined. No single case is as yet known in which such a ratio has been derived in this country. There is in this fact a certain irony which should not escape notice. For decades our game literature was largely a record of kills. If there exists, in all these tons of bloody paper, a single accurate bag count applying to a specified population or area through a period of years, then I have failed to find it. Yet these same men, every day of their lives, measured the yield of their fields, their herds, and their commerce in terms of principal and interest.

The kill of non-migratory game has sometimes been determined on *small areas*, such as quail on a given farm for a period of years (see *Game Survey*, p. 29), but the possible percentage of influx from surrounding territory is so great that a single farm is not a reliable unit. Even for a species of low mobility like quail, the determination of an accurate ratio probably requires at least five square miles. For more mobile species the area should be proportionately greater. The end-case is migratory birds, for which no unit short of the continent as a whole could be accurate.

In any and all cases, the statistics must cover a period long enough definitely to show sustained yield.

Lincoln (1930) has shown that since 1920 about 12 per cent of the ducks banded on the continent each year have been killed during the first subsequent shooting season, and points out that this is doubtless the kill-ratio (not counting cripples) for the duck population as a whole (if all the bands are turned in). The duck population as a whole, however, is quite evidently declining, so that the kill-ratio compatible with sustained yield is, under present conditions, evidently something less than 12 per cent if all the bands are turned in. If only half the bands are turned in the ratio is something less than 24 per cent. Adding an additional quarter of the kill as cripples would indicate a ratio of about 30 per cent. The waterfowl with their high breeding potential should, under management, sustain a kill of at least 50 per cent. It would appear, therefore, that management, if and when applied, should be capable of either doubling the kill, or increasing the stock, or both.

Trustworthy-kill ratios convertible to American specifications are none too abundant in the European literature. *The Grouse in Health and in Disease* says of red grouse under management in Britain:

> "In a normal season the bag will usually be about double the numbers of the winter stock, and in a very good year it may be possible to kill as many as five birds for every nesting pair" (p. 455).

Evidently the kill-ratio based on *winter* or spring census is normally 2 : 1, or 200 per cent, and runs up to 5 : 2, or 250 per cent in extra favorable years. It is the American custom, however, to census in early fall, so we must add to the spring stock not only the kill, but the unshot portion of the increase. Leopold and Ball (1931*a*), by interpolation, calculate the total fall population of the "average moor" (5–10,000 acres) described in the report as 3700 grouse, from which the usual kill is 2500. The kill ratio is therefore 2500 ÷ 3700, or about 2/3 or 66 per cent. This has been sustained on many moors since as early as 1870.

Maxwell (1911) does not give a kill ratio for managed partridges in England, but one may deduce from his acreage figures that one-half to two-thirds of the fall crop is ordinarily short, *i. e.*, 50 to 66 per cent.

Area: Kill Ratios. Reliable figures showing the kill related to area (as distinguished from fall population or census) are much more common.

Table 18 presents average yields of deer, in terms of bucks per square mile, taken from large areas through a considerable period of time. Kills from small areas during single years may be much greater. Thus Frontz (1930, p. 7) cites a single township in Pennsylvania from which 1200 deer, or 33 per square mile, were killed in 1926. This included legal does, legal bucks, and illegal kill, and is over 10 times as great as the kill from the Pennsylvania State Forests as a whole.

It is apparent that the ratios in Table 18 do not mean much as a yardstick for measuring the possible kill on some other area,

TABLE 18

AREA: KILL RATIOS FOR DEER

Size Class	Area	Period	xBucks per sq. mi. of deer range per year
Size of an ordinary state	Pennsylvania	1914-1921	0.17
	"	1922-1929	0.61
	New York	1927	0.44
	Minnesota	1919-1926	#0.44
	National Forests of New Mexico	1913-1927	0.08
	National Forests of Arizona (omitting Kaibab)	1913-1927	0.05
Size of a large county	Gila National Forest, New Mexico	1923-1927	0.17
	Gila National Forest, best part	1923-1927	0.25
	Pennsylvania State Forests	1925	2.87
	Adirondack Counties	1927	0.56
	Catskill Counties	1927	0.31
	*Stanislaus National Forest, California	1921-1923	0.55
	Santa Fe National Forest, New Mexico	1913-1927	0.02

x All ratios are obtained by dividing the kill into the actual area of deer range (as nearly as it could be estimated) producing the kill.

Plus 0.40 other deer.

* Before foot-and-mouth disease.

unless it is comparable in size and environmental conditions. Furthermore, the assumption of sustained yield is more or less unsubstantiated; thus Pennsylvania during the first period was probably understocked and during the second overstocked. The Gila Forest was once proposed as a "normal range" for New Mexico, but it has since given evidence of either overstocking or unbalanced sex and age classes. There should be developed for each set of conditions, such as a state, statistics on a truly normal area, which may serve as a yardstick for measuring the productivity of other areas of like size and kind within the same state. One of the important functions of the game-management demonstration areas now being established in Iowa (see *Game Survey and Handbook*), Michigan (Wight, 1930), and in the southern states is to build up such norms.

Release: Kill Ratios. For game annually replenished by fresh releases of breeding stock, it is important to compare the number released with the number killed. Under a stable condition, this ratio affords an index to productivity, and to the extent to which that productivity is dependent on artificial aid.

The exact meaning and value of such a ratio of course varies according to the period of years covered, the evidence of a stable condition, the time of year the releases are made (whether the released birds breed before being subjected to shooting, or vice versa), and the uniformity of distribution of the releases over the area shot. Table 19 does not pretend to iron out or define all these variables, but is intended to be merely illustrative of what a release : kill ratio looks like, what order of magnitudes are involved, and to what species it is applicable.

Banding the released birds is, of course, a more accurate method of obtaining the relationship of wild to artificial productivity than these ratios.

Yield Tables. In forestry, tables are built up in each forest region, showing the normal yield of full stands of local species for various site qualities. Similar tables would be very useful in game management, but have not yet been developed. Game yield tables should show the normal population and the normal annual yield for various qualities of range or site, in tracts of various size-classes. The following is a hypothetical example for normal yield of quail in the cornbelt. The figures for the 200-acre size-class are based on the quail census data in the Game Surveys of the North Central States (p. 38) and of Iowa. The figures for the other size-classes are estimates.

TABLE 19

RELEASE : KILL RATIOS

Species	Area	Period	#Release	Kill	Ratio
Pheasant (kill cocks only)	Pennsylvania	1915	2,096	*796	2:1
		1919	6,003	15,658	1:3
		1920	4,062	23,000	1:6
		1929	9,000	212,082	1:24
	Connecticut Public Shooting Grounds	1925	4,746	x16,196	1:3
		1926	6,157	20,291	1:3
		1927	8,170	20,415	1:3
		1928	15,077	19,828	1:1
		1929	7,500	20,000	1:3
	Minnesota	1928	3,000?	161,881	1:54?
Quail	Pennsylvania	1919	1,470	46,894	1:32
		1928-9	2,688	222,186	1:83
Wild Turkey	Pennsylvania	1919	109	5,181	1:47
		1929	150	3,834	1:26
Cottontail	Pennsylvania	1919	129	2,719,879	X
		1928-9	80,519	3,524,652	1:44

In pheasants and turkeys the numbers represent birds released plus 25 per cent of eggs given out for hatching and release.

* Pennsylvania kill obtained by assigning to non-reporting licensees the same kill as from those reporting. Resulting figures probably too high.

x Connecticut kill represents the sum of the kill by licensees actually reporting, with no allowance for those not making returns.

The table is read in this wise: A 200-acre farm is low if it has a stand of 1 quail per 5 acres or a kill of 1 quail per 15 acres. A 20,000-acre tract would class as medium, however, if it showed substantially these same figures. The 200-acre farm would be normal if it showed a bird per acre and a kill of a bird per 1.5 acres, but no large tract could normally hope to show these figures.

Effect of Management on Kill Ratio. An area which sustains a given kill without control of the other factors will obviously sustain a higher kill after the other factors have been brought under control by management. Does experience yield any clues as to how much higher?

TABLE 20

HYPOTHETICAL POPULATION AND YIELD TABLE FOR QUAIL
NORTH CENTRAL CORNBELT

Degree of stocking or quality of range	Acres Per Quail								
	200 acres			2,000 acres			20,000 acres		
	Pop.	Ratio	Kill	Pop.	Ratio	Kill	Pop.	Ratio	Kill
Low	5	1/3	15	10	1/3	30	15	1/3	45
Medium	2	1/2	4	4	1/2	8	6	1/2	12
Normal	1	2/3	1.5	2	2/3	3	3	2/3	5

Note: For tracts showing extra good interspersion, use the column to the left of that corresponding to its actual size-class. For extra poor, use the column to the right of that corresponding to its actual size-class.

The clues are scarce, because reliable measurements seldom begin until after controls have begun.

We know that red grouse under management are sustaining a 66 per cent kill, whereas a century ago without management the kill was certainly much less.

We know that whitetail deer in the Pennsylvania State Forests now sustain an area : kill of nearly three bucks per square mile, whereas a few decades ago the kill was zero.

We can conjecture, conservatively, that the present 12–30 per cent kill in waterfowl could be raised to 50 per cent by management.

DIAGNOSIS

We come now to the important process of weighing factors, or making a diagnosis of the reasons for unsatisfactory productivity.

In Chapter II game population was described as a flexible curve, which the natural increase is constantly striving to bend upward toward the theoretical maximum or breeding potential, and which the various factors are constantly striving to pull downward. Diagnosis deals with methods for determining in specific cases how hard each factor pulls downward, or which of the seven factors pulls the hardest, and why.

More than any other step in game management, diagnosis requires insight and skill. As in the diagnosis of a sick patient or a stalled motor, it is the test of the practitioner's ability to visualize the inner workings of the mechanism.

There are three essential steps in diagnosis of game productivity:

1. Visualizing the mechanism as it is, and as it should be.
2. Making an intelligent guess as to what is wrong.
3. Testing whether the guess is correct without too heavy a risk of time, funds, or damage.

If the test verifies the diagnosis, its findings may then be applied on a larger scale.

Visualizing the Mechanism; Life-Equations. The mechanism of game management is coextensive with the science of ecology. Every game manager must be a practical ecologist, but not every ecologist possesses the powers of observation essential to game diagnosis. Of all the duties of the game manager, this is probably the least susceptible of reduction to rules of thumb. All that any written text can hope to do is to state a few principles, and set down illustrative instances.

This will be attempted in the succeeding chapters, factor by factor. We are here dealing with the first step of building up, in a specific case, a mental picture of the collective operation of all the factors.

This collective action of the factors on a given species in a given locality through a typical year may be called the "life equation." I strongly recommend that the game manager, even before he has begun the process of measuring the separate factors, attempt to visualize this local life equation as a whole, and from end to end, rather than to defer thinking about any factor until he has made enough measurements to assign a local value to it, or to defer thinking about the equation until he has made enough measurements to assign local values to all its factors.

The life equation is necessarily stated in terms of a seasonal progression of important events in the animal year. It may take the form of an algebraic equation, or of an arithmetical gain-and-loss table. The latter is much simpler and just as scientific. Whatever the form, let the first attempt at an equation contain as many unknowns or guesses as need be; these imperfect figures will gradually give place to better and better actual values as the work of local life history analysis progresses.

Suppose, for instance, we are diagnosing quail on a township of land in the central cornbelt, in a state open to hunting. Let us start with 100 sample birds at the opening of the shooting season. Table 21 presents a life equation in the form of a gain-and-loss table.

TABLE 21

LIFE EQUATION FOR QUAIL

Date	Item & Computation	Gain	Loss	Current Population
On Nov. 1	Sample population	. . . .	. . . .	100
By Jan. 1	Kill=100x1/3	. . . .	33. .	66
	Crippling loss=33x18%	. . . .	7	
	Total hunting mortality	. . . .	40. .	60
By March 1	Winter loss=60x30%	. . . .	18. .	42
By May 1	(42x47.5% females=20 pairs)			
	Eggs=20x14	280 .	. . . .	322
By Aug. 1	Nest mortality=280x60%.	. . . .	168. .	154
	Hen mortality=20x14%.	. . . .	3. .	151
	Juvenile mortality apparently 151-100=51 in 8 surviving nests @ 6 per nest.	. . . .	51. .	100

The first decimation will be the kill, plus the crippling loss. We have no local values as yet for either, but we can get some by requiring authorized shooters to enter their bags in a journal. These figures will become more and more reliable as records of succeeding years pile up. For the present, in order to clarify our evaluation of the other factors, we will use *temporary values* obtained by analogy. Let us say that the present stocking seems low. For a poorly stocked area of this size class Table 20 indicates a kill-ratio of 1 : 3. We will arbitrarily assume a kill loss of $100 \times 1/3 = 33$ birds, leaving 66. For the crippling loss we will use the average for quail in Table 17, even though it applies to a different species. This is 18 per cent of the kill of 33 birds, or 7 birds, a total probable hunting mortality of 33 + 7 = 40, leaving 60 surviving on January 1.

This brings us to the period of winter loss through starvation and predators. Errington's studies (1930) in nearby Wisconsin showed a loss of 30 per cent in *isolated* covies during the normal winter of 1929–30. Our covies are less isolated (and therefore probably on less adverse range), but until we know something better we will use his figure as it stands. The assumed winter loss is therefore 30 per cent of 60, or 18, leaving 42 birds surviving on March 1.

We must here bear in mind that whatever the correct average winter loss may be, it is going to fluctuate greatly with weather, food, and predator conditions from year to year.

This brings us to the nesting season and the as yet unmeasured phenomenon of pairing. The local sex ratio is as yet undetermined, but Table 12, gathered in this same region, shows an average of 52.5 males to 47.5 females. Theoretically, therefore, our remaining 42 birds ought to make about 20 pairs. Actually we are not sure that all birds pair off, so our actual pairs may be somewhat less than 20. On the other hand, we know that some pairs, after losing their first nest, will try again, and that our nesting mortality data will apply to this gross number of nests, rather than to the net number of pairs. In other words, there are more nests than pairs. In the absence of better information, we may assume that these two errors balance each other, and that our 20 pairs will lay and hatch 20 nests of 14 eggs each, which, after adding the parents, makes 322 actual and potential birds. The figure 14, as representing the eggs per clutch, is Stoddard's Georgia average shown on Fig. 3.

This brings us to the three most difficult unknowns: nest mortality, hen mortality, and juvenile mortality. There is no local information on what values to assign. Stoddard (p. 196) found the nest mortality in Georgia to be about 64 per cent, due mainly to predators, and to abandonment of nests induced by predators or accidents. This percentage is very probably subject to large local variation. At the outset, however, it is the best figure we have, and would indicate a loss of about 60 per cent × 280 = 168 eggs, which reduces the population to 154.

About 20 per cent of Stoddard's total nest mortality of 60 per cent was due to abandonment, which, except for weather, was probably principally due to the loss of the hen. We may therefore set down very roughly a hen mortality loss equal to ⅔ of the abandoned nests, or 14 per cent of our 20 paired hens, or 3 hens, leaving 151 birds alive at the time of hatching.

Even Stoddard was unable to measure juvenile mortality. It is so difficult to observe that it may always have to be measured by getting the best possible values for the other losses, and then arbitrarily calculating what it ought to be if next fall's population is the same as this fall's. In our table it apparently ought to be about 151 juvenile birds. These must be lost from the surviving nests, which comprise only 8 of our original 20, or an average juvenile loss of 6 per surviving brood of 14 each.

Table 21 obviously by no means constitutes a true picture of what actually happens on our sample area, but rather merely a background by which we may measure the significance of our local facts as we discover them from time to time, and by which we may predict what "leaks" are the most in need of measurement. Suppose, for instance, next fall's hunting statistics indicate the usual kill to be 50 per cent instead of 33,—the significance is that one or more of our assumed values for winter loss, nest mortality, or juvenile mortality are too high. Or suppose that an actual study of nest mortality next year shows only 30 per cent loss instead of the assumed 60 per cent,—the significance is that one or more of our assumed values for the other losses are too low and need checking, or else that there is something wrong with our assumption that the two errors mentioned on the preceding page balance each other.

Almost every project in game management or game research is constantly confronted by difficulty in deciding which of two or more jobs is the more important. No field worker possessed of any imagination at all can possibly perform more than a small fraction of the jobs in sight at any one time. Constant reference to the life equation may yield an obvious answer to questions of job priority which might otherwise be puzzling and obscure. He may, for instance, have thought of a new way to get more accurate statistics on crippling loss, and at the same time of a new way to get more accurate statistics on nest mortality. No probable error in Table 21 could be great enough to obscure the fact that the latter job is ten times more important than the former.

The magnitude of losses, as roughly pictured by a life equation, also enables the worker to make important inferences as to their probable exact cause. Thus a juvenile mortality of two or three birds per average brood might readily be ascribed to accident, whereas the indicated mortality of six per average brood almost certainly implies that some predator or even disease has been at work.

The foregoing illustrative exercise in the use of the life equation for the diagnosis of factors in a given case has assumed for simplicity that the fall population remains constant from year to year. In actual practice this is seldom the case. The skillful manager will make further inferences from the character of the year in which the fall population is greater or less than normal. If, for instance, it rises above normal after a mild winter or a dry summer, the inference is obvious. If it falls below normal after a flight of goshawks or a year of overshooting, the inference is equally obvious. There are almost endless possibilities in this process of inferring cause and effect from the aggregate behavior of the game population, interpreted in the light of a gradually accumulating series of measurements.

Matching Factors; Natural Experiments. The use of the life equation for visualizing the collective operation of the factors throws important light on *when* the heaviest losses occur, but only inferentially on what factor is responsible for each item of loss. The second step consists of guessing which factor is limiting, and the probable relative weights of the other factors.

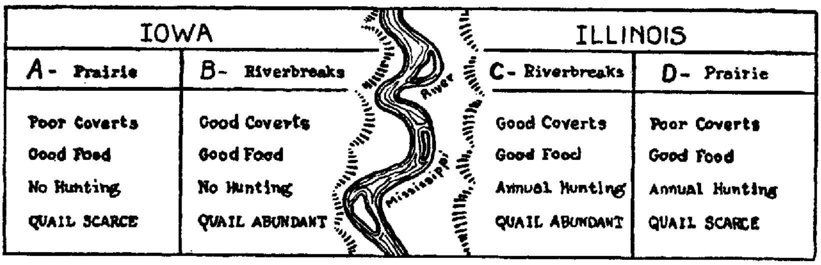
Such a guess should start with the question of whether all of the seemingly suitable units of range are occupied. If any seemingly suitable range unit is unoccupied, then the indication is that some factor subject to wide local variation is responsible, or else that the stock has been reduced to the point where it cannot fill up any but the choicest ranges, or else that our information as to what constitutes a suitable range is wrong.

If all the seemingly suitable range is occupied, but by too thin a population, then the indication is that the limiting factor is of wide and relatively uniform distribution. From this character it may be possible to infer its identity.

Such inferences may sometimes be checked by finding two places where the suspected factor differs, but where the other factors are seemingly alike. A comparison of their populations will substantiate or refute the importance of the suspected factor. In other words, we look for a pair of accidental or natural experimental plots, in which all but one variable has been accidentally matched out, and we measure their respective populations to check our inference. The reliability of conclusions drawn from such natural experiments will vary directly with the skill of the observer, and often, I think, with the size of the areas compared. The smaller the pair of areas the harder it is to be

FIG. 18

MATCHING FACTORS

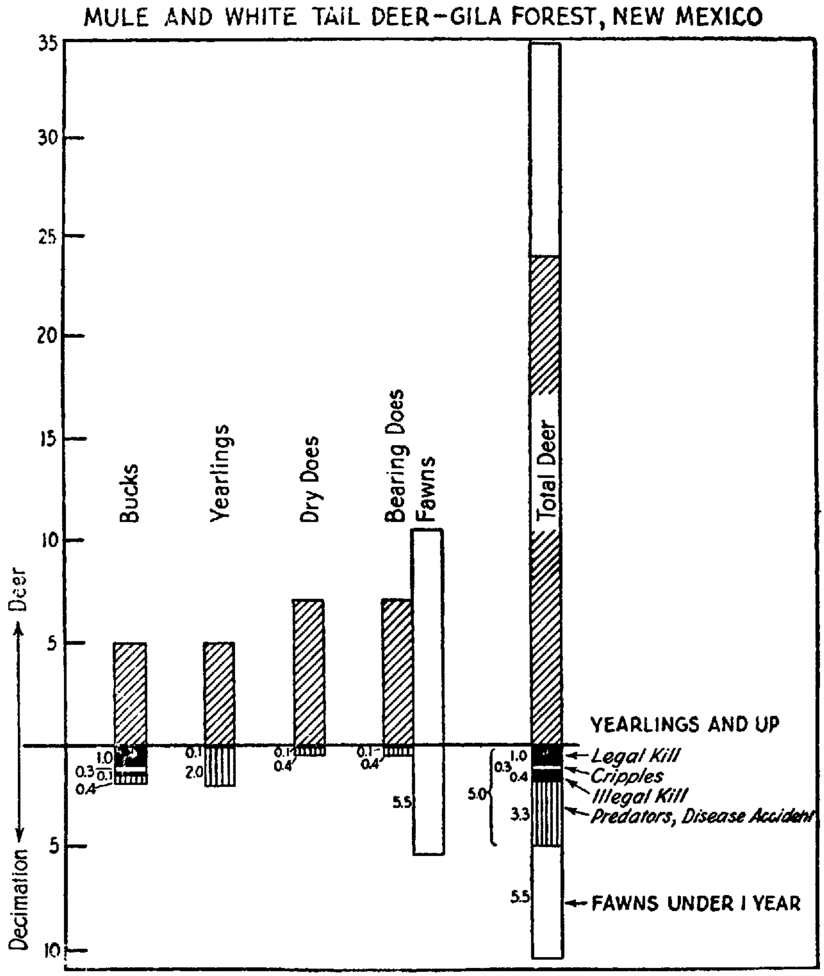


sure that there is only one important variable. On larger areas the extraneous variables will tend to average out, provided the variable which the investigator has in mind is quite uniform in its distribution. To avoid the necessity of describing too much detail, a generalized question on a rather large pair of areas will be used for illustration.

Let us assume that the question to be checked is whether coverts or hunting are the limiting factor for quail in northwestern Illinois. We must look, then, for a pair of areas where the same intensity of hunting applies to good and poor coverts respectively, and for another pair where similar coverts are subjected to heavy and light hunting respectively. Large paired areas answering the first specification can be found in many places where the prairie type, which is almost devoid of coverts, borders upon the river-breaks of the Mississippi, in which brushy areas and ungrazed woodlots still persist, and are quite uniformly distributed. Food conditions are in general good in both places, which are diagrammatically portrayed in Sections *D* and *C* of Fig. 18.

FIG. 19

CALCULATING UNKNOWN FACTORS BY SUBTRACTION



The second specification would be hard to find on the Illinois side, but easy if both sides of the Mississippi be considered. On the Iowa side of the Mississippi the same transition from good to poor coverts occurs (see Sections *B* and *A*). There has been no legal quail hunting in Iowa since 1916. If it be true that the prohibition of quail hunting on the Iowa side has been actually enforced, then we have in this transect of the Mississippi, representing four combinations of hunting and coverts, a natural experiment in which all factors except hunting and coverts have been accidentally matched out. A measurement of quail abundance would in most places show *B* and *C* to be equally good, and *A* and *D* to be equally poor. A day's work with a good dog in Sections *B* or *C* will, during a normal year, usually show seven or eight coveys, while the same kind of work in Sections *A* or *D* will seldom show more than two or three. In all four sections coveys will occur only in or near brush coverts. To the extent, therefore, that our premises and measurements are correct, the conclusion may be drawn that cover and not hunting is the limiting factor for quail in this geographic region.

Graphic Evaluation of Unknowns. In some instances the values of certain factors are known, and the resultant of all of them is susceptible of measurement at some particular stage of the life equation. In such case the sum of the unknowns can be easily determined by simple subtraction, graphic or arithmetical.

Fig. 19 portrays a sample graphic subtraction. In deer, and in most other game animals not reaching maturity before the second year, the annual increment to the breeding population is represented by the proportion of yearlings, and this proportion can, in the more open types of range, be approximately determined by tallying large numbers of animals as seen on the range. On the Gila National Forest, New Mexico, such a range tally was made by forest officers co-operating with the Sportsmen's Association of Southwestern New Mexico. The results are shown in terms of a "unit herd," which is the herd producing one killable buck per year,—in this case 24 deer. The height of the bars above the horizontal line shows the composition of this "unit herd" of 24 deer by sex and age. Excluding fawns less than one year old, yearlings were found to comprise 5 of the total number of 24, or 20 per cent.

It is axiomatic that *the number of fawns reaching the yearling stage is equal, in a stable herd, to the total annual decimation among deer older than yearlings,* which is to say that the number of fawns reaching the yearling age is equal to the sum of all the decimating factors among the older deer.

It is also axiomatic that *the difference between the number of* *fawns born and the number of yearlings surviving is the total annual decimation among fawns.* The number born was approximately determined by range tallies just after the fawning season to be 10.5 for each 24 deer.

It follows from the first axiom that if we add up the values of all the known factors among the older deer, and subtract their sum from the number of yearlings, the difference equals the sum of the unknowns. The known legal kill is 1 buck; the estimated crippling loss 0.3 bucks; the estimated illegal kill 0.1 buck, 0.1 yearling, 0.1 dry doe, and 0.1 bearing doe, or 0.4 deer; the total known decimation is thus 1.7 deer. Subtracting this from the annual increment of 5 yearlings, we get 3.3 deer per year (per unit herd of 24) as the sum of the values of the other decimating factors (predators, disease, and accidents) which is the unknown we started out to find. Probably the bulk of this loss of grown deer may be ascribed to predators.

It follows from the second axiom that the fawn decimation from all factors is $10.5 - 5 = 5.5$.

The essential conditions for applying this method of "analysis by subtraction" is that the annual increment be known, and that the values of some of the subsequent factors of mortality be known. The difference will always be the value of the other factors. The difference between the increment and the breeding rate will always be the juvenile mortality. The classification of the population into sex and age classes is not essential. Any unit of population may be used, provided it be self-contained and stable. Decimation may be expressed in per cent instead of absolute numbers. Arithmetic is as good as a chart, but is probably less easily visualized.

The method could readily be applied to game birds if grown young could be distinguished from adults by plumage, weight, or other suitable criteria, and their proportion determined.

Tests of Diagnosis; Effects of Dilution and Influx. It is seldom advisable, even after making the best-founded guess as to the factor set-up in a given problem, to proceed at once to convert that guess into full-scale action. It is always advisable first to test the diagnosis by means of small-scale experiments. Caution is necessary, not only because the guess may be wrong, but also because the isolation of a limiting factor and the proposal to control it usually does not establish the best *method* of controlling it, or the *degree* of control necessary to accomplish the desired purpose. For both these purposes small-scale tests are necessary.

The first question to come up in testing a diagnosis is the size of the test area. This must always be definitely related to the characteristics of the species involved, especially their mobility. Thus, a 160-acre area to test the effects of controlling mobile hawks and owls would be absurd, while the same size might be ample to test the effects of controlling non-mobile skunks. The difference would be the greater mobility of the hawks and owls. The question of size boils down to a question of boundary dilution. Hawks and owls would "leak in" around the boundary of a 160-acre tract in a day or a week, whereas skunks might not leak in during the course of a year.

Boundary dilution of the game itself may also mask the effect of a test, if the area is too small. The more mobile the game, the larger must be the test area. Restoring the coverts or food on a test area of 160 acres could with certainty be expected to bring about a measurable response in quail population, whereas the beneficial effects of a test of the same size on prairie chickens might be immediately diluted over a whole township, and hence be too small to measure.

Influx may likewise make the results of a test appear greater than they actually are Improvement of cover and food, for instance, on a 160-acre test area might bring about a winter influx from surrounding territory, hence a winter census might appear to show a response greater than what was actually secured on the test area, or greater than what would be secured if the improvements were later extended over a whole township.

Susceptibility to Control. Effective diagnosis of factors must take into account economic as well as biological limitations. On most areas game is a by-product or secondary crop, hence management measures which might be biologically correct would be useless if they cost too much, or if they interfered with the primary crop. For instance, in north central New Mexico the following diagnosis was made for scaled quail: it was observed that quail were most abundant along the boundary between irrigated fields offering food, and uncultivated brushy mesas offering cover. Grazing was the principal industry on these mesas, and ranch headquarters and stock water were almost all located on the same boundary favored by quail, *i. e.*, between the fields and the foothills. Hence the intensity of grazing reached its maximum at this boundary.

The critical season for cover was plainly winter, and at this season it was observed that practically all quail coveys not actively feeding were resting under a certain species of bush called chamisa (*Atriplex* sp.). This bush was also a favorite winter browse for cattle, and hence had been reduced from former abundance to one or two bushes per 40 acres.

A diagnosis of this quail problem from the viewpoint of quail alone would have indicated the total exclusion of grazing from a strip of mesa paralleling the fields. The local economic system, however, made its execution impossible, hence the recommendation was *to fence individual chamisa bushes* with very small gateless fences from one to three rods square. This recommendation was never actually tested, but it is almost certain that the protection from grazing of even one chamisa bush per 40 acres would have resulted in a vigorous response of the bush, and the formation of a stiff dense evergreen umbrella-like covert. This might readily have brought about a perceptible increase in the quail population density.

Indices in Diagnosis; Buck Shortage. Sometimes a certain condition suspected of affecting productivity is not susceptible of measurement or even observation, but some other condition *related to and varying with it* is susceptible. In such event the latter may be measured as an index to the former.

Thus in bobwhite, if a disturbed sex ratio were suspected but circumstances prevented measuring it, the frequency of whistling (unmated) cocks might serve as an index to excess males.

Distribution is often an excellent and accurate index usable in the diagnosis of food, water, and cover questions. Thus one would not have to observe feeding habits or measure crop contents to learn that northern bobwhites live on corn and ragweed in winter. The winter distribution of coveys almost proves it. This is also a good example of how, through the use of an index, it may be found out whether a fact established by research for one region holds good for another region.

In diagnosing deer herds, the game manager encounters among laymen a belief that "buck shortage" is responsible for unsatisfactory productivity. Buck shortage cannot be measured directly without an elaborate and expensive range tally of sex and age classes, and in brushy ranges this is impossible. Even if the game manager can find out, through a range tally, what the buck supply is, he may not yet know with any great certainty what it ought to be. Is there any index which could be used to throw light on such a situation?

It seems probable that three indices could be developed for detecting buck-shortage: (1) diameter of antler beam in the bucks killed, (2) points per head or per antler in the bucks killed, and (3) dispersion or spread of the fawning dates.

In each case the index condition for the range suspected of buck shortage would have to be compared with the same condition for a similar range known to be normal or believed to be normal.

As already pointed out in Chapter VI, Cahalane has developed antler beam as an index to age. It is likely that a subnormal proportion of bucks would be associated with some abnormal proportion of age classes. Hence comparison of antler beams in the kill from normal and suspected range might serve as an indicator of buck shortage.

The comparison of antler-point classes in the kill, illustrated in Fig. 17, might serve the same purpose provided old bucks with decreasing points can, on the range in question, be safely assumed to be scarce enough not to distort mass data.

Fritz, in *The Pennsylvania Deer Problem* (1929) evidently suspects (although he does not positively assert) that buck shortage prolongs the rut. This, if finally substantiated, would automatically disperse the fawning dates. Such dispersal would be readily observable, and any two ranges could be compared by expressing a large number of observations on fawning dates as frequency curves.

Where does are legally shot, and where the open season follows the rut (as it does in most eastern states), a direct anatomical examination of large numbers of does is of course the most direct possible index to buck-sufficiency. This index was used by Fritz during the emergency doe season in Pennsylvania. Usually, however, does are legally protected, in which event this method is inapplicable.

Summary. Productivity is the kill or increment per unit of population. When the population cannot be measured, the kill per unit area is used.

Measurements can be compared with breeding potential, or with those from standard or normal units. From the latter, standard yield tables could be drawn.

The crippling loss must be added to the kill to get the decimation by hunting. It is from 10 to 100 per cent as large as the kill.

The kill in waterfowl is possibly 30 per cent of the population, in red grouse 66 per cent, in English partridge 50 to 66 per cent.

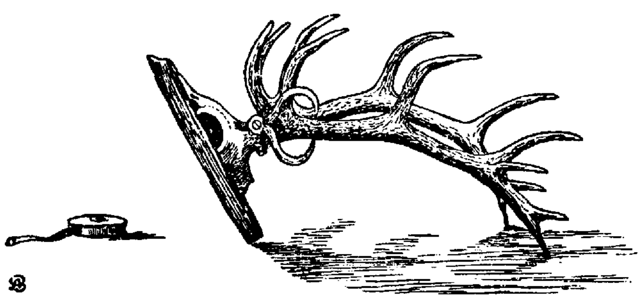
The area-kill in deer runs from 2.87 bucks per square mile downward to nearly zero.

The number of birds artificially released, as related to the kill, yields a useful ratio.

Diagnosis should begin with a life-equation showing progressive mortality, in so far as known. Unknown factor values can sometimes be inferred from natural experiments, or, where the increment of young is known, by graphic subtraction.

Diagnoses should be tested on a small scale before full-scale controls are attempted. Influx on small-scale tests may prove confusing. Indices may be used for diagnosis in some cases.

This chapter describes the periscopes wherewith we attempt to see and measure the net results of the tragedies which transpire daily behind the veil of greenery where game lives and has its being. To see the unseen has become a commonplace in modern science. Game managers, as well as physicists and chemists, can do it.



Chapter VIII

GAME REFUGES

This, and several subsequent chapters, deal with the manner in which the factors operate and the actual execution of the control measures indicated by the processes of measurement and diagnosis.

Usually each control measure has for its objective the control of a single factor. For instance, laws are passed to control hunting, trapping is undertaken to control predators, plantings are made to alter food or cover. Each of these distinct categories will be the subject of a separate chapter. There is, however, one important device, namely the game refuge, which affects many or sometimes all of the factors in a given case. This chapter deals with the technique of game refuges, and the factors which can be controlled through their establishment.

Definitions. Unfortunately current usage has so confused the meaning of the term "refuge," in its relation to other terms, that any discussion of the subject must begin with a series of definitions.

A game refuge is an area closed to hunting in order that its excess population may flow out and restock surrounding areas. A refuge is at all times a sanctuary, and the two terms are synonymous.

The surrounding area may be a shooting ground, and the primary objective of the refuge may be to maintain a breeding stock on that shooting ground. A refuge may, however, fulfill the same function in the case of a closed species on which there is no legal shooting. It is nevertheless properly called a refuge because it functions through the same fundamental mechanism of outflow.

No area is properly called a refuge, however, which is not surrounded by range suitable for the species in question. A refuge, in short, is an integral part of a larger area, performing for that larger area a definite function by reason of its closure to hunting. Normally that function is to supply an outflow of breeding stock. It may, however, be to provide a resting place. Refuges for migratory birds are often located outside the breeding range, in which event the sole function is to provide a rest ground, or a place for unmolested feeding, or both. In other cases the function may be to prevent the extermination of the species until it has recuperated sufficiently to resume the process of flow.

A refuge is not the only kind of an area closed to shooting. A game reservation, for instance, is an area closed to shooting, but isolated either by reason of unsuitable surrounding territory or by reason of enclosure, thus bearing no functional relationship to its immediate surroundings. Its function is to reserve or perpetuate some particular species.

The term "preserve" is properly applied to any shooting ground, either public or private, but usually private. It may or may not include one or more refuges as a part of its working mechanism.

A "park" in the rural sense is a reservation dedicated not only to game but to other natural attractions. Its function is public recreation and education. A park often produces a flow which restocks surrounding hunting ground in the same manner as a refuge, but this function is incidental and does not constitute its primary purpose.

Mechanism of Game Refuges. The foregoing definitions establish the essential character of a refuge, namely a place which provides sanctuary, breeding ground, or some other essential service, and thus enhances the productivity or abundance of game on the surrounding range. The services may differ, but the result is always an outflow of breeding stock.

Breeding stock does not flow out from any area unless there is population pressure within the area, or unless the range outside is better. There can be no population pressure within a refuge without law enforcement and the control of predators, food, cover, or any factors which may be holding down productivity.

The number of head which will flow out depends on the intensity of the population pressure within, and the distance to which the excess population will flow out varies with the mobility of the species. Any species, no matter how low its mobility, will of course flow into favorable vacant territory in the course of time. The flow from a refuge, however, depends mainly on the annual mobility rather than the long-time spread-rate. If the surrounding territory suffers from lack of breeding stock, it usually suffers every year and must be replenished every year. The effective radius of a refuge, therefore, is the distance to which it will spread breeding stock *annually*.

Certain definite corollaries now follow from the above definitions and from the preceding discussions on the properties of species.

The size of a refuge suitable for a given species should, for instance, not be smaller than the unit range for that species, unless it is intended as a rest ground only.

The distance apart must not be greater than twice its annual mobility, *i. e.*, the outflow from two adjacent refuges should meet annually at a point theoretically half way between them.

The kind of land selected for the refuge must be capable of correcting the primary defect of the surrounding range. If this is overshooting, the refuge must be located where the game is located during the shooting season. In species which perform either an altitudinal or a latitudinal migration, this is usually distinct from the breeding grounds. If, on the other hand, the primary defect of the surrounding range is lack of breeding ground, the refuge should be breeding ground.

Some early attempts to establish refuges in the national forests proved ineffective because the main need was protection from hunting, but the refuges were located on the breeding grounds. In polygamous species, like pheasant and deer, where males only are legally taken in hunting, it is often less necessary to provide breeding refuges than to provide an irreducible residuum of males. If closed seasons cannot be enforced sufficiently to protect the females, it is seldom likely that the addition of a new and localized closed season (in the form of a refuge) will do any better.

Sometimes, as in southwestern deer, the bucks and does occupy more or less distinct localities during the hunting season. Some of the early refuges on the national forests had to be moved, because they were found to include only doe range.

Good cover is almost always an essential in refuges. In pheasants, for instance, the refuge should provide swamp cover from which the birds cannot be routed by hunters.

Refuge Patterns. It follows from the foregoing discussion that a system of refuges for one particular species of game should be laid out according to a geographic pattern, wherein the size of each unit and the distance between units are adapted to the characteristics of that species. It also follows that the pattern best for one species will not be best for another, and may even be unsuited for the other.

Thus if bobwhite quail have an annual radius of 2 miles, there should be one refuge in the centre of each 4-mile square, *i. e.*, 1 for each 16 square miles of range, or about 2 or 3 refuges per township, or about 40 refuges per county, or about 4000 per state. These figures are premised on the normal cornbelt pattern of square counties containing about 16 townships each and about 100 counties per state.

If whitetail deer have a unit range of half a township and an annual radius of 6 miles, then a system of deer refuges should show about 1 for each 12-mile square, which is equivalent to 4 per county, or 40 per state.

If ducks have a unit range (in the sense of the minimum area from which they cannot be flushed from the boundary) of 100 acres, and a daily radius of 25 miles, then a system of rest grounds should include at least one 100-acre refuge per 4 counties, or 20 per state.

Twenty refuges per state for ducks or 40 for deer is a possibility; 4000 for quail is a pipe-dream.

The actual patterns of the most advanced deer refuge systems tend to approach these theoretical patterns. Figs. 20 and 21 show the existing refuge systems in Pennsylvania and New Mexico. In both cases the pattern is essentially that required for deer and turkey, and properly so. In New Mexico the waterfowl refuges represent a separate and distinct system along the main rivers. In neither state is there as yet in existence any comprehensive refuge system for small upland game of low cruising radius.

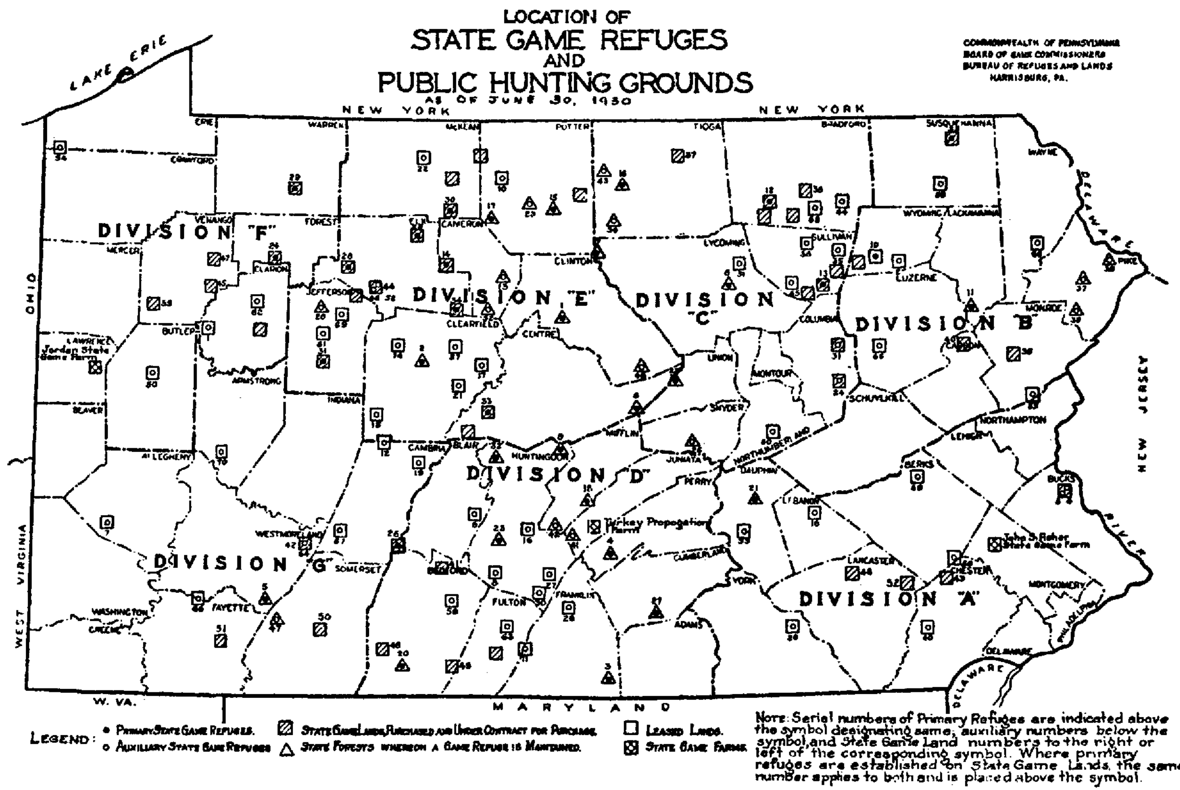
Extending the Radius of Refuges. It is well-nigh impossible for a state either to acquire or administer the hundreds of refuges indicated as a necessary pattern for non-mobile species like bobwhite quail. Such refuge units are too small and too numerous to be susceptible of public administration, and, as will appear later, the land is often too costly for public purchase on any such scale.

It is, however, entirely practicable to extend artificially the

Fig. 20

As of June 30, 1930

Reproduced by courtesy of Pennsylvania Board of Game Commissioners.



radius of effectiveness of quail refuges by annually trapping the excess population and planting it as breeding stock in the same manner as pen-raised or imported quail are now planted. Such wild-trapped native stock probably has a higher survival value than either pen-raised or imported stock, and the cost per pair ought to be much lower, although it cannot as yet be said that this has been proved. Such a refuge for the production and trapping of breeding stock has the same function as a game farm, but productivity is obtained by improving the natural environment, rather than by confining the breeding stock under wire. The method is adapted not only to quail, but to almost any species which can be readily trapped. Trapping the excess followed by immediate replanting dispenses with any need for storing the trapped birds in pens. They may be shipped directly to the point of release, and immediately turned down. Grange (1930) first proposed this method for the production of Hungarian partridges in Wisconsin. Oklahoma has since adopted it for quail, and Iowa for Hungarians. There seems little doubt that the high cost of imported stock can thus be radically reduced. This method is preferable to the prevalent practice of importing Mexican bobwhite.

Species Suited to Refuges and Public Shooting Grounds. On private preserves or clubs there need be no difficulty about designing a refuge system suitable for any species of game, even the least mobile. The refuges may be made as small and as numerous as necessary without extra cost, because the refuge is under the same pre-existing administration as the surrounding shooting grounds.

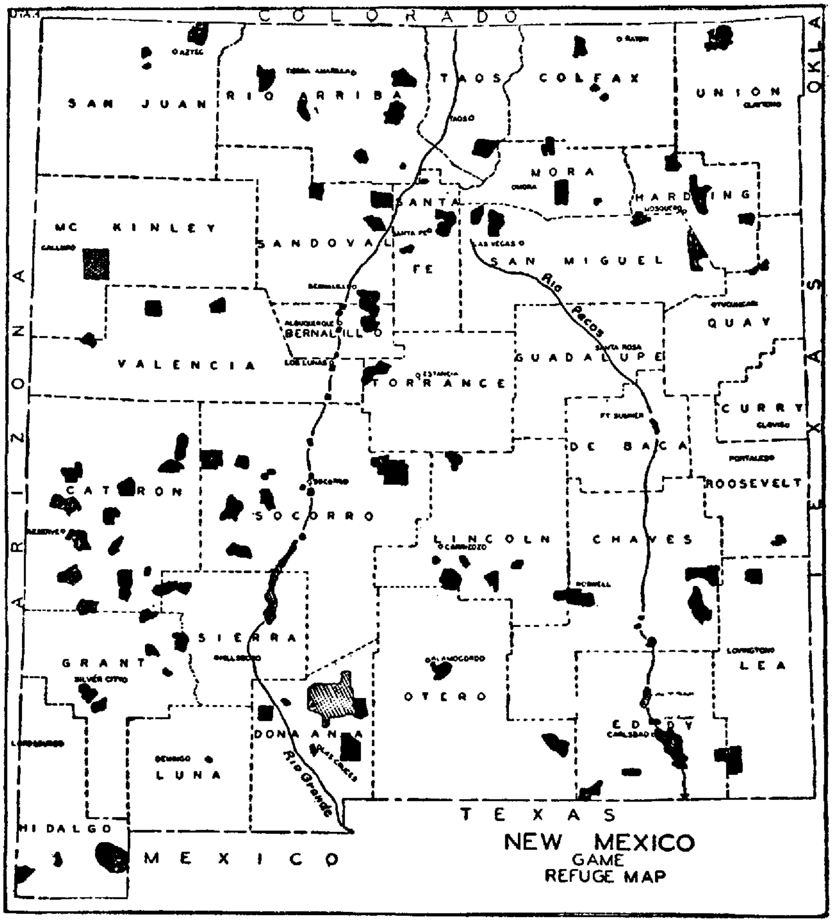
In the case of waterfowl there is likewise no difficulty in designing a refuge system for any public or private shooting ground, provided only the ground be large enough to contain room for at least one refuge.

Where it is proposed, however, to set up public refuges for the less mobile species, for the purpose of restocking surrounding public shooting grounds by natural outflow (as distinguished from trapping), the game manager's verdict should be given with caution, and only after weighing the characteristics of the particular species in relation to the character and cost of the land. Many such proposals are well intentioned but impracticable, and lead ultimately to disillusion.

FIG. 21

GAME REFUGE PATTERN IN NEW MEXICO

(Reproduced by courtesy of State Game Commission)



Note: The refuges along the two main rivers are for waterfowl. Being on "navigable water," they are in public ownership.

The other very small refuges are experimental refuges for quail, mostly in private ownership. The remainder are big-game refuges for deer, turkey or antelope, mostly on the National Forests.

The large blank areas without refuges are gameless plains, mostly federal public domain, and gameless Indian Reservations.

The game, to stand up under such a system, should first of all have a high radius, both annual and daily. Without high daily mobility, it will not readily seek sanctuary from a considerable distance, and without high annual mobility the outflow of breeding stock will not take place.

Second, the game should be of a species tolerating high populations per acre, otherwise the acreage of land necessary to produce a given annual kill becomes excessive.

Third, the species should preferably not be cyclic, especially if the land be expensive. Carrying costs during the lean years of the cycle may prove heavy.

Fourth, the species should be able to endure a heavy kill. Polygamous species are especially advantageous, since in them a large part of the males may be removed as kill without damaging productivity at all.

Fifth, the species should, if possible, be susceptible of artificial propagation, so that should the breeding stock be overkilled it may be pieced out by artificial plantings.

Sixth, and most important of all, the species should be a skulking one, not susceptible of total annihilation in good cover.

In addition, the practicability of any system may be tested by a seventh criterion as to land. The land must be cheap in relation to its game-carrying capacity, and available in blocks of sufficient size. If lands acquired for some other public function, such as forests, are obtainable, so much the better.

Migratory waterfowl rate very high, especially under points 1, 2, 3, and for some species, 5. Their ability to benefit from refuges is outstanding and well known. (See Miner, 1923.) Their adaptability to public shooting grounds is not so obvious, but with proper regulation of the total volume of shooting may be regarded as distinctly hopeful, even though not wholly proved (see Leopold, 1926, and Lloyd, 1923).

Table 22 gives some rough figures comparing pheasants, cottontails, quail, and whitetail deer and turkey as to their adaptability for public shooting grounds kept stocked by an interspersion of public refuges.

Table 22, in conjunction with what every one already knows, shows why the pheasant scores very high on points 1, 2, 3, 4, 5, and 6. The pheasant's weakest point is 7, the species usually requiring good land.

TABLE 22

SUITABILITY OF UPLAND SPECIES FOR PUBLIC REFUGES
SUITABILITY OF UPLAND SPECIES FOR PUBLIC SHOOTING GROUNDS

Species	Cruising Radius, Miles		Land Value	Max. Distance Apart, Miles	Rating
	Day	Year			
Pheasant	1/8-1/2	1/2-3	$25-$50	5-10	3
Cottontail	1/8-1/4	?	$25	4	4
Quail	1/8-1/4	1/2-3	$25	4	5
Whitetail Deer	2	6-15	$5	15-20	1
Wild Turkey	1	4	$5	10-15	2

Species	Max.Pop. Per Acre	Max.Kill Per Acre	Per Hunter			Restocking Cost (Per Head)	Fluctuation of Population
			Kill*	Acres to Yield	Land Invest.		
Pheasant	1.0	0.7	5	7	$300	$2.50	10%
Cottontail	4.0	3.0	10	3	$75	$1.00	50% ?
Quail	1.0	0.5	10	20	$500	$6.00	50%
Whitetail Deer	?	0.005	1/3#	66	$330	$20.00	10%
Wild Turkey	?	?	1/3#	66 ?	$330 ?	$10.00	50%

* Assumed bag per year per hunter sufficient to sustain his interest and support.

Reduced for success ratio of 3 hunters per buck killed.

It also shows why the whitetail deer scores very high on 1, 3, 6, and 7, and moderately high on 4. The deer's weakest point is 2. Most other species of horned game share these characteristics of deer. Turkeys are also weakest on 2.

The quail's weak points are 1, 6, and 7. The cottontail outscores quail on 2 and 6. His weak point is 1, low mobility.

The central columns of Table 22 require some explanation. Take pheasants for example: The possible stand is a bird per acre, and the possible kill is three-quarters or 0.7 birds per acre. If the average hunter is satisfied with 5 per season, it would require 7 acres of refuge to produce them, assuming all the breeding to take place on the refuge. This is, of course, a severe assumption, but is made in all species merely for uniformity. If the land for the refuge costs about $40 per acre (see Table 22*a*) a fixed investment of about $300 *in refuge land* (not counting public shooting ground) is necessary. This is a lenient assumption.

In general, pheasant, deer and turkey are the species which most nearly meet the specifications in their entirety. A classification of refuge functions for deer is given in the *Game Survey*, pp. 241–245. It may be said without hesitation that of the various upland species, they are the best adapted to public shooting grounds.

Several other upland species seem well adapted to profit from refuges, especially prairie chicken and sharptail grouse. Both score well except on points 3 and 5. The sharptail excels the chicken on 7. The ruffed grouse is high on 6 and 7, but low on 1, 3, and 5.

Such actual experience with upland game as has so far accumulated strongly substantiates these ratings. The principal success of Pennsylvania's state-owned refuges and shooting grounds has been with deer, and of her auxiliary refuges with pheasants (see Phillips, 1922; Coffin, 1928; Conklin, 1930). New Mexico has an effective system of public refuges (state) and shooting grounds (National Forests) for deer and turkey (see Ligon, 1927), and the same is true of deer and other big game in various degrees in the other western states. Michigan is gradually building up a system of state deer refuges and public shooting grounds on an especially sound basis (see Biennial Report for 1927–28).

Refuges for Cyclic Game. Refuges can furnish protection against hunting, predators, or starvation, but not against disease. They have seldom been employed for cyclic game. Would they work?

There are two opposing ways to regard this question. One is that by speeding up recovery of normal density after decimation by disease, a refuge system would lengthen the peak period and thus improve shooting.

The other is that by speeding up recovery, the density assumed to be requisite to a new outbreak of disease would come sooner, the cycle would be shortened, and shooting injured or at least not improved.

The second seems the more probable from the theoretical standpoint. Practical experience, however, points toward the first as the best supported by evidence. As already pointed out in Chapter III, the British grouse cycle does *not* seem to have been shortened by inducing speedy recovery of normal density. Moreover thin populations do not seem to be immune when the cycle hits. The high mobility of at least certain cyclic species (such as prairie chickens) would tend to give a rapid spread to the increased population, and thus tend to prevent overcrowding of the refuge itself.

In short, as nearly as we can guess in the present state of knowledge, refuges might lengthen the peak period by at least a year or two at its anterior end.

Sample Pheasant Refuge. Fig. 22 presents a concrete illustration of how the principles set forth in this chapter can be applied in a particular case. This refuge is designed to be a combination refuge, winter feeding station, winter covert, and (in so far as possible) nesting covert for pheasants in the prairies of northwest Iowa where nesting cover is probably the limiting factor, followed by winter cover and winter food in order of importance. There should be at least one in each township. The map is reproduced and the following explanation quoted from the Handbook "*Management of Upland Game Birds in Iowa*" (1932).

"The refuge is best built around some gravel pit, slough, marshy lakeshore, ditch junction, or other parcel of idle or cheap land where some cover already exists and more can be developed. The gravel pit offers cheap land and a south-facing bank, while the willow thicket and cat-tail bogs offer cover.

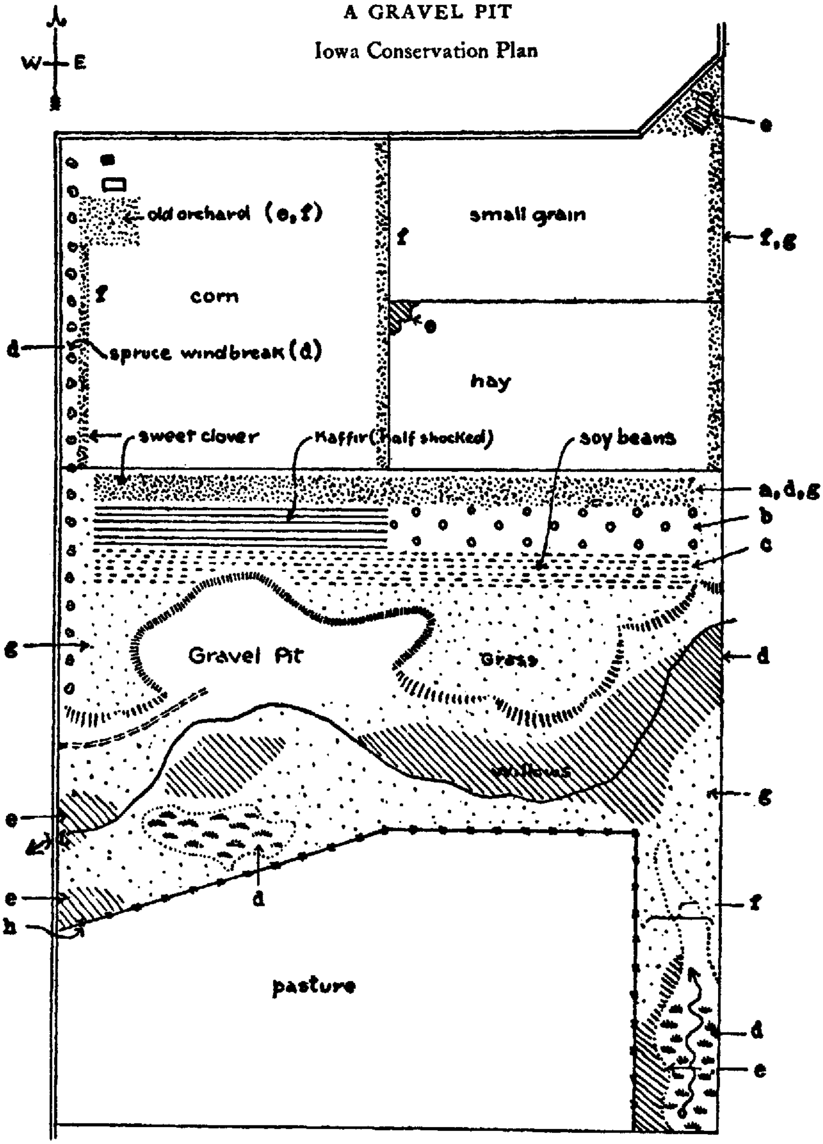
"The pit is first of all fenced to exclude grazing (*h*). The level part is planted to (*a*) sweet clover for snow cover and nesting, (*b*) kaffir, sorghum, corn, or other grain for food, and (*c*) soy beans or weedy fallow for more food. *A*, *b*, and *c* are rotated from year to year. Half of the grain is left standing for fall food, and the other half shocked so that a new shock can be opened with each winter storm. Without this precaution the food is likely to be eaten up before the 'pinch period' arrives.

"No refuge can nest as many birds as it can winter. In order to extend the nesting capacity as far as possible, small clumps of brush for crowing grounds (*e*) are developed in corners of surrounding fields, each adjacent to fencerow strips (*f*) of uncut hay, small grain, grass, or weeds for nesting. This system of crowing grounds and nesting strips should be extended into the surrounding farms as far as possible.

FIG. 22

PHEASANT REFUGE AND FEEDING STATION DEVELOPED AROUND A GRAVEL PIT

Iowa Conservation Plan



a, b, c: crops, to be rotated
d: snow cover
e: detached units of cover for crowing grounds
f: travel lanes
g: nesting cover
h: new fence to exclude grazing

"A coniferous windbreak should be added along the west side of the refuge for winter cover and wind protection."

Future Use of Refuges. The device of refuges is like any other device in game management—it presents no magic formula which can be counted upon to build up any species of game in any environment. Its successful use depends on knowing when not to try. A tragic waste of enthusiasm and funds has often followed blind reliance on refuges.

If the *American Game Policy* (1930) correctly gauges the future, it may safely be predicted that refuges will play an important rôle in the future management of migratory game, forest and range, and wilderness game, but not in farm game. Refuges are necessary for the successful management of migratory game and of big game on both public and private lands, because in all these the amount and distribution of hunting is hard to control. On the other hand, they will hardly play a large rôle in the management of farm game, where the amount and distribution of hunting may be limited at will by the farmer, and must be so limited in any event. Where hunting is under full control, there is little occasion for refuges.

Summary. The basic function of a refuge is to produce an outflow of game to surrounding range.

Outflow arises from population pressure within, and varies with the mobility of the species. Refuges should be as large as the unit range of the species and not over twice its radius apart. This implies a characteristic pattern for each species and terrain.

In a quail pattern the refuges are too small and numerous to be practicable units for public administration. Successful deer patterns have been developed in several states.

The effective radius of a refuge can be extended by trapping and replanting the excess stock.

The criteria of suitability in species for refuges and public shooting grounds are: high mobility, high density limits, absence of cycles, capacity to stand a heavy kill and be artificially propagated, skulking habit, and low-priced land. Waterfowl, deer, turkey, and pheasant rate the highest.

Refuges hold little promise of utility for management of farm species other than pheasants.

Chapter IX

CONTROL OF HUNTING

THEORY

Purpose and Premises. As long as game shortage prevails, the purpose of hunting controls is obviously to limit the kill of each species on each parcel of land to its productive capacity. As its capacity is increased by the control of hunting and of the other factors, an increase in the kill may be permitted.

After game shortage has been corrected by management, the purpose may extend beyond mere limitation. It may become necessary actually to enlarge the kill in order to bring the game into a desirable relationship to farm or forest crops, or to regulate its kind and distribution so as to bring about a better or more uniformly distributed stock. In this country, however, these problems of holding down the game lie mostly in the future.

The present problem divides itself into two different but equally difficult parts:

1. To devise mechanisms for limiting the kill on areas under public management.
2. To devise mechanisms which will encourage private owners to limit the kill on their own lands as the first step in private management.

Suitable trespass laws for encouraging the private landowner to exclude unpermitted hunters are an essential first step toward the solution of the second problem. By suitable is meant laws which prohibit hunting without the owner's permission, and which do not require the owner to prove damage in order to prosecute trespassers. All of the succeeding discussions are premised on the assumption that such laws exist. Without them, it is hopeless to expect many private landowners to limit the kill, or otherwise to practice game management.

Kinds of Control. There are three basic sources of control for the hunting factor.

The first is to restrict the time, place, purpose, amount of kill, method of hunting, number of hunters, or species hunted by the exercise of public compulsion in the form of group rules or police power.

The second is to create an incentive for the hunter or the landowner to limit hunting in these same ways, by the voluntary exercise of restraint based on self-interest.

The two contrasting methods may be called for short the "restrictive" and the "incentive" methods, respectively.

Restrictive control requires only legislation and enforcement.

Incentive control, on the other hand, while it may be encouraged by legislative enactments, must have its origin in the enthusiasm of the hunter, or the landowner's interest in profits from the sale of shooting, or in the game for himself, or in the opportunity for dispensing hospitality to his friends.

Cutting across both of these fundamental sources, and exerting a large potential influence on both, is a third source of control arising in the individual ethics of the hunter. Many game laws consist essentially of the exercise of police power in support of average individual ethics. The most advanced individuals, however, often adhere to self-imposed restrictions which go farther than the law, and farther than group rules.

Adaptation to Landownership; Psychology. The fundamental principle which must govern the regulation of hunting is that the average human can be induced to conserve voluntarily what stays on his own land so that it is available for his own use, but only the exceptional individual will voluntarily conserve what he shares with the community at large. It follows that voluntary restraint in hunting can be depended on mainly for non-mobile game (*i. e.*, farm game as defined in Chapter V, and other classes to the extent that they occur on inhabited private land), while compulsory restraint, or restriction, must mainly be relied on for mobile game, and game on public or uninhabited lands. This includes all migratory game, all wilderness game, and much forest and range game.

The fundamental defect of present hunting controls is that they have ignored this distinction.

The possible field of voluntary or "incentive" control can be considerably enlarged by encouraging the organization of neighborhood groups, thus making each member of the group feel a selfish interest in game too mobile to stay on any one member's land. Thus a farmer with 100 acres sharing 100 prairie chickens with 5 individualistic neighbors is going to "get his share," while the same farmer as a member of an organized group which has agreed on certain restraints might regard the same birds as partnership property, to be husbanded like his personal property. This principle, too, has been until very recently ignored.

Incentive for restraint can also be strengthened by disseminating reliable technical facts on what rewards will follow specified restraints or efforts.

The effectiveness of compulsory or restrictive control can likewise be enhanced by "education," and by skillful devices for bringing into play the forces of *amour propre*, and the forces of competition. Some progress has occurred here. Thus some refuges of small size and high visibility enforce themselves, because the hunters keep watch on each other. Most closed seasons are enforced by mutual watchfulness. It may safely be said that no restriction can be enforced by police officers alone, no matter how much legislation or money be poured into the attempt.

Legislative controls bear the flavor of compulsion by absentees, whereas all the others represent self-initiative or group-initiative of some sort. These psychological attributes have an important bearing on enforcement.

In short, the attempt to control hunting has suffered from ignoring economic and psychological facts, and their varying relation to local conditions. It has especially suffered from the persistence of the concept that all hunting is the division of nature's bounty. We must replace this concept with a new one: that hunting is the harvesting of a man-made crop, which would soon cease to exist if somebody somewhere had not, intentionally or unintentionally, come to nature's aid in its production.

Indirect Controls; Diminishing Returns. Our present restrictive game laws do not regulate the kill per year from each unit area. Obviously the basic objective of controlling hunting is to limit the kill to the productivity of the land. Since this varies greatly as between localities, and since restrictive controls regulate the kill only according to time, purpose, method, and species, they do not directly accomplish the basic objective. The issuance of "limited licenses," in which the number of licenses is limited to a fixed maximum, is one exception, but since this device is applicable only to big game in isolated herds hunted by absentees who can be checked in and out of the area, it hardly invalidates the general conclusion.

The contention of protectionists (such as Hornaday, 1931) that game can be and in some cases is being virtually exterminated by the sheer numbers of perfectly legal hunters is only too well taken. If we limit remedial action to the traditional restrictive controls, then their contention that more restrictions are the only remedy is also well taken. If, however, we can increase the resistance to hunting by improving the environment, and limit the amount of hunting to the productivity of each unit of the land—in short, if we can develop game management and the incentives to practice it—then there is a hopeful prospect for accomplishing directly what restrictive controls have so far vainly sought to bring about by indirect methods.

What the protectionist rightly asks is how management can be tried out without relaxing the restrictive controls now in effect. A later caption tries to answer this question.

Hunting as now "controlled" in most states would have long since decimated many additional species, were it not for the "law of diminishing returns" to which the hunter's effort, like all other efforts to make land yield an increase, is subject. When game becomes scarce there is an automatic tendency for hunters to hang up their guns, and thus reduce the kill. The more prized the species, the more tardy the operation of the law. The more extensive the equipment necessary for its pursuit, the more prompt the operation of the law. The virtual disappearance of both quail hunting and bird dogs from some "shot-out" quail states is a case in point.

Balancing Species and Systems. It is too often assumed by sportsmen that a system of hunting controls which results in something to shoot is *per se* a satisfactory system. In the long run, no system is satisfactory which does not conserve the rich variety of our game fauna, as distinguished from merely its most resistant and "shootable" species. This is one (and by itself sufficient) reason for not relaxing the idea of public control in seeking to develop private incentive for game production. Landowner initiative, left wholly to its own devices, would inevitably tend to sacrifice the unprofitable to the profitable forms of wild life. It would tend unduly to sacrifice migratory to resident, non-game to game, and predatory to game species. For these reasons sound public policy must seek to encourage and develop private incentive *without relaxing* restrictive safeguards. This is often no easy matter, especially where restrictions have so narrowed legal seasons that the bona fide producer of game has insufficient time to harvest his crop, or worse yet, is prohibited from harvesting it at all. Possible solvents for this difficulty are suggested in the later section on technique.

HISTORY

Attitudes Toward Hunting. A disinterested observer, viewing the history of game management in America from some vantage point offering both intellectual and chronological elevation, would, I think, be forced to regard our efforts so far as a failure, noble in motive but awkward in execution. With the advantage of both hindsight and foresight, his diagnosis of the present situation would call for:

1. Maximum development of incentive for restraint.
2. Control of the other environmental factors, as well as more effective control of hunting.

The present conservation public is far from appreciating the need of these corrections in game policy. Many sportsmen still habitually place the blame for game shortage on "vermin" or "politics" or even on "too many restrictive laws." Many non-shooting protectionists, with equal regularity, place the blame on "too many sportsmen." Such verdicts are hardly entitled to be called diagnoses. The wish is too obviously father to the thought. They represent merely the age-old insistence of the human mind to fix on some visible scapegoat the responsibility for invisible phenomena which they cannot or do not wish to understand.

Up to the time when modern biological techniques were brought to bear on the diagnosis of game questions, such attitudes were excusable. At the present time, however, there is probably no instance of game shortage, the reasons for which could not be found and weighed by scientific investigation, and hardly a state which does not contain within its own borders the man-power and funds requisite to a substantial diagnosis of mooted game questions. The trained man power, however, is busy with the biology of anything but game, the money goes for stop-gaps, conservation factions nullify each other, and game policies continue to be "worked out by rule of thumb, by practical politicians and business men."

One school of thought among present-day sportsmen proposes to abolish restrictive controls almost *in toto*, and hopes, by authorizing the sale of game and encouraging artificial propagation, to develop sufficient private commercial incentive to offset the need for restriction. This doctrine ignores the biological fact that such incentives are largely inapplicable to mobile, migratory, and public land game. To sacrifice one class of game in the effort to produce another is hardly a satisfactory solution of the problem.

Development of Controls to Date. The lopsidedness of hunting controls thus far developed in this country is indicated by Table 23. It is evident from the table that restrictive controls have ramified into infinite detail, while incentives for the production of game, and for restraint in its harvesting, have experienced only the most rudimentary development. With the exception of one or two states which have passed "shooting preserve laws" authorizing more liberal hunting privileges on land artificially restocked, there is not a single move toward the most obvious of all ways toward building incentive: allowing land which is "sown" proportionate privileges in "reaping." These laws constitute our preliminary gropings for some practical method of rewarding effort or restraint, and of penalizing sloth or excess.

Our present game laws have developed some ingenious devices for indirectly reducing the total volume of kill. Many states deliberately set the open season on deer so that snow and cold will keep all but the hardiest hunters at home. Several states, such as Michigan, set the prairie chicken season at a late fall date in order to take advantage of the well-known fact that these birds are very much harder to kill late than early in the autumn. The present impetus toward the establishment of refuges, often regardless of whether they fit the species or the conditions, may also be construed as an indirect attempt to limit the kill.

Trend of Seasons and Bag Limits. That the present system is steadily trending toward the radical shortening or total closure of open seasons for hunting is clearly shown in Fig. 23, which summarizes the trend in the eight north central states since 1900. The "curves" for the separate species simply connect the points of change in open seasons. The figures adjacent to each curve show the accompanying shrinkage in bag limits. It goes without

TABLE 23

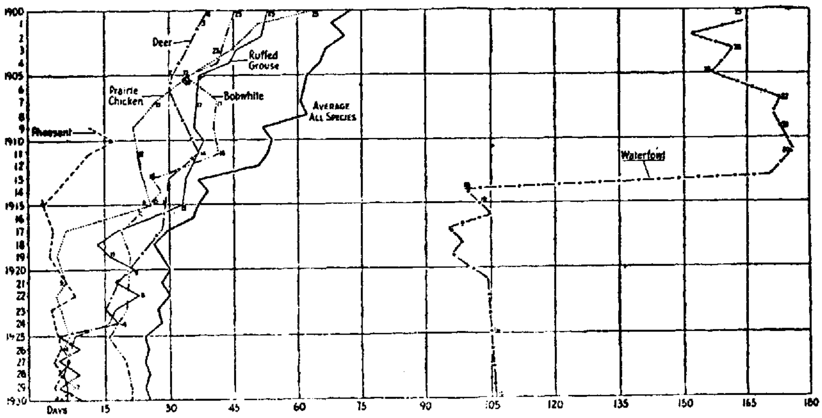
HUNTING CONTROLS SO FAR DEVELOPED

			Vehicle of Expression & Enforcement			
			Public		Private	
			Laws & Regul.		Group	Individual
Class	Kind of Control	Method	State	Fed.	Rule	Ethics
I.	RESTRICTIVE CONTROLS					
	Time of Hunting:					
	Period	Open & closed seasons	X	X		X
		Confinement of self-hunting dogs in nesting seasons	X		X	X
	Days of week	Rest days, Sunday laws	X		X	
	Hours of day	Sunrise & sunset rules	X	X	X	
	Place of Hunting:					
	Locality	Refuges	X	X	X	
	Region	Closed counties	X	X		
	Cover	Open water laws	X			
	Landownership	Trespass laws	X			X
	Purpose:					
	Market hunting	Non-sale laws	X	X		
	Propagation for food	Tag laws	X			
	Kill:					
	Amount per day	Daily bag limits	X	X	X	X
	Amount per season	Season limits	X			X
	Kind (as to sex)	Buck & cock laws	X			X
	Kind (as to age)	Length & no. of prongs	X			X
	Method of Hunting:					
	Dogs	Anti-hounding laws	X			
	Conveyance	Motor boat, airplane, sink box, battery, auto	X	X		X
	Armament	Gauge, no. of shots, decoys, nets, traps, etc.	X	X		X
	Number of Hunters:	Limited license	X	X		
		Allotment of blinds			X	
	Species to be Hunted:	"Songbird" lists	X			
		Proscription lists	X		X	X
		Closed species	X	X		X
II.	INCENTIVE CONTROLS					
	Authorizing Special Season on Restocked Lands	Shooting preserve laws	X			
	Authorizing Charges but Regulating Rates	Licensing of preserves	X			

saying that this continual shortening of open seasons reflects not merely a decrease in game, but a corresponding shrinkage in the availability of hunting as a source of recreation for the average citizen. We must, of course, shrink open seasons and bag limits to what the game can endure, but in doing so we should clearly realize that we are likewise shrinking its recreational value. The problem of game management is to build up the game so that the continuance of that shrinkage becomes unnecessary. The problem of hunting controls is to devise such relationships between landowner and sportsmen that longer seasons will not necessarily mean excessive killing.

FIG. 23

SHRINKAGE OF OPEN SEASONS AND BAG LIMITS IN THE NORTH CENTRAL STATES



(The curves show by years the average number of days open season allowed for each species. The figures adjacent to each curve indicate progressive changes in daily bag limit. A separate curve shows the average open season for all species. In figuring bag limits states totally closed and states with no bag limits have been disregarded.)

The chart does not include the shortened waterfowl season of 1931. The fact that seasons and bag limits on migratory birds have remained so much more liberal than seasons on resident game strongly substantiates the assertion made elsewhere in this chapter that people can be induced to conserve what stays on their own land, but only the exceptional individual will voluntarily conserve what he shares with the community at large.

TECHNIQUE

The technique of restriction is too well known to require exhaustive presentation. The technique of building and regulating incentive is largely non-existent, so that most of it must be left to future writers on game management. The present volume can only suggest some devices for getting facts, describe some typical situations, and suggest some general principles for the guidance of game administrators and managers.

Control of hunting on private lands in a single ownership is no problem. The game manager simply stipulates, within the limits of the law, what and where his guests or members can shoot.

Control of hunting on public lands is not so simple. One starting point for hunting controls on public game ranges, or private co-operative projects, is to determine what the average hunter gets. This must always bear some relation to what game management may hope to provide for him.

Success Ratio. While present laws limit neither the total volume of kill, nor its distribution in accordance with the productivity of unit areas, there is nevertheless on large areas a quantitative relationship between the number of hunters and the volume of kill. The statistical determination of this relationship, which may be called the success ratio, is possible only where the kill has been measured, and this is so far seldom done except on big game. Table 24 gives some examples of success ratio for big game on large areas.

The success ratio is often remarkably stable from year to year. Thus on the Gila Forest, where the 5-year average is 2.4 hunters per buck, the lowest year showed 2.1 and the highest 3.1. In Minnesota, where the 8-year average is 4.0 hunters per buck, the lowest year shows 3.4 and the highest 5.5.

A success ratio is very valuable in operating the plan of limited licenses. For instance, if it were desired to limit the kill on the Gila to about 500 bucks, the issue of licenses should be limited to $500 \times 2.4 = 1{,}200$ licenses.

Success ratios for small game are very hard to get, because under our present "system" neither the kill nor the number of hunters on any given area are usually known. Michigan, by a special questionnaire, determined that 265 ruffed-grouse hunters, in the field for 3 days each in 1930, put up 11,000 grouse and bagged 1248, or about 4.7 grouse per hunter per season, or a little over 1 grouse per hunter per day. In 1929 the bag was about 4 grouse per hunter per season, or 1.3 grouse per hunter per day.

TABLE 24

BIG-GAME SUCCESS RATIO

Area	Species	Period	Length of Season, Days	No. of Hunters per	No. & Kind of Game
Gila Forest (New Mexico)	Mule & White-tail Deer	1923-7	10	2.4	1 buck
	Turkey	1923-7	10	13.0	1 turkey
Kaibab Forest (Arizona)	Mule Deer	1926	30	1.1 ?	1 buck
Wyoming	Moose	1926	?	1.1	1 bull
Pennsylvania	Whitetail	1924		3.0	1 deer
		1926	15	6.0	1 buck
New York	Whitetail	1927	30	11.2	1 buck
Minnesota	Whitetail	1919-26	21	4.0	1 buck
		1919-26		2.1	1 deer
California	Mule & Black-tail Deer	1928	15-30	4.9	1 buck
		1929	15-30	5.4	1 buck
Average of above for buck deer				5.0	1 buck

During both these years grouse were about "halfway up" on the cycle of increase. The bag limit was 5 per day and 10 per season.

The Iowa Game Survey determined, by questionnaire, the success ratio of 129 parties of pheasant hunters in Iowa during the 2-day open season of 1931. In 5968 man-hours of hunting 11,230 pheasants, or 1.88 per man-hour, were put up, and 2964, or 0.5 per man-hour, bagged. Assuming a full 6-hour day, this means a bag of 3 per day. The legal limit is 3 per day or 6 for the season. Of course, the actual hours hunted were often less. The average hunter just about secured his limit.

Shooting journals of individual sportsmen furnish an individual success ratio which may or may not be representative, depending on the individual's marksmanship, equipment, and ethics, and the kind of ground hunted. Table 25 presents some samples which may illustrate the disparity between "the old times" and the present, and between regions and species. The Pringle snipe bag may excite curiosity. Details are available in Phillips (1930, p. 123).

Many shooting journals suffer in their statistical value because the bags given are of the party, rather than the individual gun, and the actual hours in the field are not specified. The journals quoted in the table are free from the former error, but some are open to the latter.

TABLE 25

INDIVIDUAL SUCCESS RATIOS

Name	Place	Period	Species	Days Hunted	Kill Total	Kill Per Day	Kill Per Yr.
Arnold Seagrave	Rhode Island	1895-1930	Ruffed Gr.	*382	784	*2	24
J. J. Pringle	Louisiana	1874-75	Jacksnipe	42	6,615	157	6,615
A. W. Schorger	Wisconsin	1921-29	Jacksnipe	42	214	5	24
Aldo Leopold	Wisconsin	1924-29	Jacksnipe	*46	279	*6	46
Donal H. Haines (See Leopold, 1930)	Michigan	1918-29	Jacksnipe	180	300	2	27
E. J. Nelson (Game Survey, p. 211)	Wisconsin	1921-28	Ducks	62	291	5	36
Aldo Leopold	New Mexico	1917-23	Ducks	*97	570	*6	81
		1917-23	Quail	*28	391	*14	56
		1917-23	Doves	*33	742	*22	106

* Fractional days converted to whole days of about 8 hours each.

Average Bag. There is another type of ratio which cannot properly be called a success ratio, but which is nevertheless valuable for comparing hunting conditions between different states, and between different times in the same state. This is the ratio of general license-holders to total bag, from which can be derived the average annual bag per license. It differs from Table 25 in that not all of the license holders hunted the species in question, but merely purchased general licenses which entitled them to do so. Table 27 gives the average bag for Minnesota as a sample. Average bags cannot, of course, be derived in states which do not require licensees to report their kill.

The figures since 1924 were derived by making a proportional allowance for the bag of licensees not reporting. The percentage making a report is decreasing. The method of computation previous to 1924 is not known. Conflicting figures have often been published by the state during recent years, hence the consistency of the table is not vouched for.

The grouse bags clearly show the cycle. Note the high bag 1920–24, and closure or low bags since. Also note how awkwardly the "alternate year" plan meets the actual conditions, the season being closed in 1921, when grouse were abundant, and open in 1926, when they were scarce.

TABLE 26

AVERAGE BAG, 1931, WISCONSIN, 120,897 REPORTS

Game	No. Killed	Kill Per Hunter
Waterfowl	350,500	1.9
Ruffed Grouse	38,900	0.3
Prairie Chicken	36,000	0.3
Cottontails	1,074,500	9.0
Snowshoes	366,500	3.0
Squirrels	453,000	3.8

Total head per hunter. 19.3

The average bag of waterfowl indicates a decrease in kill, in spite of improvements in armament and transport.

The only consistent increase is in pheasants, but the average hunter gets less than two cocks per year.

Wisconsin inaugurated a similar report in 1931. Returns have been received from three-quarters of the total licenses. The figures are not directly comparable with Minnesota, because no allowance is made for non-reports (see Table 26).

Licensed Projects; Differential Privileges. One promising device for encouraging private initiative in game management without losing public control is the licensing and regulation of certain private ventures which exclude the general public, or which charge the public for hunting privileges. By penalizing undesirable practices, and rewarding desirable practices on such licensed premises, a flexible and powerful force for private game conservation could be brought into play.

TABLE 27

AVERAGE ANNUAL BAG, MINNESOTA

Year	Per cent Reporting	Small Game Licenses	Waterfowl Killed	Waterfowl Per Hunter	Cock Pheasant Killed	Cock Pheasant Per Hunter	Ruffed Grouse Killed	Ruffed Grouse Per Hunter	Prairie Chicken Killed	Prairie Chicken Per Hunter
1919	?	76,426	1,805,000	24	closed	X	closed	X	closed	X
1920	?	72,344	1,415,000	20	closed	X	501,500	7.0	closed	X
1921	?	114,443	1,041,000	9	closed	X	closed	X	176,700	1.5
1922	?	114,823	1,555,000	12	?	?	550,000	4.8	closed	X
1925	?	88,336	1,335,000	15	closed	X	closed	X	328,900	4.0
1924	?	139,580	1,348,000	10	?	?	352,200	2.4	closed	X
1925	56	132,196	1,322,000	10	closed	X	closed	X	412,000	5.1
1926	50	126,903	2,189,000	17	40,023	0.3	200	0	closed	X
1927	40	125,520	1,119,000	9	closed	X	closed	X	?	?
1928	40	141,097	1,550,000	11	161,881	1.1	closed	X	closed?	X
1929	?	110,536	1,500,000	14	closed	X	closed	X	10,547	0.1
1930	25	185,825	2,400,000	15	268,340	1.5	closed	X	closed	X

The "shooting preserve laws" recently enacted in several states may be regarded as one of many potential applications of this principle. (See Mich. I. W. L. A., 1930, and Wisc. Cons. Dept., 1932.) These laws are an attempt to meet the all-too-common predicament of private groups which are ready to produce game, but which are confronted by an open season too short to make it worth while. To such groups the state says in substance: "Go ahead and produce some pheasants; our warden will count what you liberate, and we will then allow you a special season to shoot a specified proportion of what you turn out. But we will license you, and reserve the right to close you down if you abuse your privilege. You must tag your kill so it can be identified at all times."

Such laws are so far limited to pheasants, because a release of pen-raised pheasants can be accurately counted. If the principle can ultimately be extended to wild-raised game, including native species, its usefulness and significance will be much enhanced. Such extension of course implies the availability of wardens skilled in game census, and able to judge the adequacy of management measures on the ground; it also implies continuous and accurate kill records, so that overshooting can be detected and penalized.

Iowa Permit Plan. This is in effect a proposed extension of the shooting preserve principle to wild-raised game, but it differs from the usual shooting preserve laws in one other important respect: it deals exclusively with farmers or farm groups, rather than with leasees of shooting privileges on farms.

The proposed statute reads:

> "The Commission is authorized to issue permits to landholders or groups of landholders to conduct experiments, in co-operation with the State Agricultural College, for the purpose of determining whether the game on lands owned by them can be conserved by the practice of game management. Such permits may authorize the taking of the estimated annual surplus of any species of game produced on the permitted area, including protected and closed species, under such conditions as the Commission may specify. Each permit will specify the species to be taken, the maximum number of each, the season during which they may be taken, and the bag limit per person per day. No permit shall be issued or renewed until the area has been inspected by the Commission for the observance of the game laws and the conditions of the permit. No game shall be removed from any experimental area, or held in possession therein, without affixing to each head a non-reusable tag, such tags to be issued by the Commission at ten cents each."

The steps in the operation of the proposed permit system would be about as follows:

1. A group of farmers owning, let us say, 1500 acres, organize, post their lands, and install food and cover improvements of the kind described in the *Iowa Handbook.*

2. Within, let us say, two years they have built up a strong stand of game. They apply to the Commission for a permit to harvest the surplus.

3. A trained game manager inspects the area and makes a census. He finds, let us say, 1000 birds on the 1500 acres, and that food and cover are good. He recommends a permit to shoot 400 birds.

4. The Commission asks the Agricultural College for a check on the Inspector's findings. Their biologist O.K.s them.

5. The Commission issues a permit to the farmer organization to harvest 400 birds during the next ensuing fall, with season,

bag limit, etc., specified. The permit is accompanied by 400 tags.

6. The farmers' organization conducts the shooting under such terms as it sees fit. It may elect to confine the shooting to its members, or to invite friends, or to sell a part of the shooting privilege.

7. Immediately after the shooting the inspector makes a new census to see if plenty of breeding stock is left, how many tags were used, and in general whether the shooting has been conducted with due respect for the conditions of the permit and the interests of the public. If so, he recommends renewal for the following year. If not, he tells the farmers what is wrong, and that a renewal may be expected only when conditions have been corrected.

He also advises the farmers on possible further improvements in food, cover, or control of hunting. If in doubt on any biological question, he calls on the biologist from the College for advice.

The *Iowa Handbook* says: "The purpose of this proposed enactment is to work out a practical way for the state to reward enterprise in game management without relaxing its protection on unmanaged areas. It offers a promising way to authorize limited hunting of quail and Hungarian partridge, and also to extend pheasant hunting to those parts of the state where regular open season would risk undue depletion of the birds."

It goes without saying that this "permit system" would be dangerous except in states which have equipped themselves with

1. A technically minded Commission, reasonably free from political influence.
2. A trained staff of game administrators.
3. A biologist trained in game management and attached to some impartial disinterested institution.

The obvious intent is that the permit system shall grow until game cropping becomes widespread.

The underlying advantage over the shooting preserve principle is in the lower costs and superior quality of the crop. No one has yet devised a way to turn down pen-raised game at less than a dollar or two per head, and such game, aside from its chicken-wire "flavor," is too expensive for the ordinary citizen to shoot. Wild-raised game under the permit system ought seldom to cost more than a half or a quarter as much.

The principle of licensing might well be used to accomplish state regulation not only of farmer-groups engaged in game management, but also landed shooting clubs or other groups which exclude or charge the general public, or which control more than a specified area. In any list of such organizations, there are always some which are progressive and inclined to respect the public interest, and others which are the opposite. At the same time there is a growing list of practices which need to be regulated, but which do not lend themselves to rigid statutory enactments, or inflexible regulations. Baiting, installation of club refuges and rest periods, and shooting methods and equipments, are examples. A licensing system, backed by authority to close down on failure to comply with reasonable license stipulations, would be one way to exercise public control in all such matters.

Such a licensing system of course implies a technical competence and stability which does not yet exist in most state conservation departments.

Controls on Public Areas. The recent trend toward acquiring and managing public shooting grounds is laudable in its democracy, but limited in its possibilities of expansion by the lack of any workable device for preventing overshooting. As long as any bearer of a hunting license can shoot any public area as long as his time and his shells hold out, subject only to the open season and the bag limit, just so long will successful management on such areas be handicapped. Such unregulated public grounds will fail except on land too poor or inaccessible to be in demand, or on species so resistant as to stand the pounding, or so mobile as to tap the surrounding supply. Refuges scattered over the area are only a partial answer. The system contains the seeds of death.

Several ways of correcting or mitigating this handicap ie ready at hand.

One is a nominal charge per-man-per-day, to help defray the expense of acquisition and operation of the area.

Another is a check-in and check-out system limiting the use to be made of the area by any one individual.

Another is to close the area as soon as the safe kill for the year, or the safe allotment of hunters, has been reached.

Another is a lottery to decide who may hunt, the officer in charge to say where and how much.

Non-Game and Protected Species. The presence in the field of large numbers of hunters, especially when coupled with scarcity of legitimate game, aggravates the killing of non-game species and rare protected species, laws to the contrary notwithstanding.

In the case of some non-game species, this is condoned as "vermin" control. The problem of "vermin" is discussed under the chapter on predator control.

Many species are thus killed, however, which cannot possibly be called predatory. Such killing is a direct and serious injury to those who derive enjoyment from seeing these species alive, and this includes many sportsmen. Such killing is bad management because it is bad esthetics. Control of the killing of non-game and protected species constitutes a distinct and important part of the general problem of hunting controls. The problem is nowhere as yet satisfactorily solved. The present legislative prohibitions are a good starting point, but do not alone constitute a remedy. Neither does education alone constitute a remedy—it is too slow. It is possible that some of the developments under Incentive Controls will offer opportunity better to protect the public interest in non-game species. For instance, all private ventures in game management licensed by the state (and many of them will eventually have to be licensed for one reason or another) could be forced to observe a reasonably enlightened attitude toward predators, other non-game species, and closed species of rare game, under pain of non-renewal of license.

Hunting Accidents. While game productivity and sound esthetics are ordinarily the sole objectives of management, there are an increasing number of situations where human safety, as threatened by hunting accidents, must partially determine the system of hunting controls.

Table 28 indicates the prevalence of such accidents in Pennsylvania as recorded by the Game Commission. This is a good sample state, because of the diversity of its game and game ranges.

Those accidents not self-inflicted (66 per cent of the Pennsylvania total for 1925–29) are in the average state undoubtedly aggravated by congestion of hunters, which in turn is aggravated by the short open seasons associated with lack of game due to lack of management, and lack of control of hunting. If the total volume of hunting were regulated as to time and place, by proper organization of both state and private game ranges, there would be no need for very short seasons, and hence a lesser concentration of hunters and fewer accidents.

Primitive Weapons. In the development of sporting methods, there arise from time to time groups of individuals who voluntarily limit their armaments to simple or primitive weapons, with the idea of making sport more difficult.

TABLE 28

NUMBER OF YEARLY HUNTING ACCIDENTS IN PENNSYLVANIA

Period	Self-Inflicted		Inflicted by Others		Total		No. of Hunters Licensed	Licenses Per Accident
	Fatal	Non-Fatal	Fatal	Non-Fatal	Fatal	Non-Fatal		
1930	23	77	36	214	59	291	536,394	1:1530
1925–29	28	73	25	170	53	243	500,886	1:1690
1920–24					40	115	475,521	1:3080
1915–19					28	94	316,811	1:2600
1913–14					24	77	302,000	1:3000

Analysis of 1930 Accidents

	Per cent during Small Game Season	Per cent during Big Game Season
Fatal	19%	81%
Non-Fatal	14%	86%

	Per cent caused by Rifles	Per cent caused by Shotguns	Per cent caused by Revolvers
Fatal	4%	12%	0
Non-Fatal	16%	67%	1%
	20%	79%	1%

At the present time such a group is devoted to redeveloping the art of hunting big game with bow and arrow. In some states pressure is being exerted to open refuges to bow and arrow hunting, or to provide special areas open to bow and arrow only, where bowmen will not be placed in competition with guns. Other groups using other primitive weapons may arise in the future and make similar demands.

Such demands might possibly be accommodated in the marginal areas, not quite favorable enough to stand up under ordinary hunting, but nevertheless sufficiently productive to stand up under hunting with less destructive weapons. Such areas are commonly located comparatively near to centres of population, and cannot be opened up to regular hunting without being over-run and shot out. Reserving them for primitive weapons may be a solution.

Deterioration Through Hunting. In some instances hunting controls must seek to safeguard not only the numbers but the quality of the breeding stock.

Hunting of small game is usually not selective of the best individuals, and hence involves no danger of racial deterioration, except indirectly through possible over-control of selective predators. Sex selection is sometimes practiced consciously, as in cock laws on pheasants, and sometimes a slight degree of it is practiced unconsciously, as pointed out for Georgia bobwhites in Chapter IV. There is no reason to suppose that these sex selections are racially dangerous.

In hunting antlered big game, however, a deterioration in size and apparently in genetic quality has been observed to follow long periods of trophy hunting. A Boone and Crocket Club committee is compiling *Records of North American Big Game* in which the measurements of notable trophies will be recorded. A tentative report states:

> "The present day wapiti heads, whether due to restriction of the winter range, diminished herds from which to select trophies, or intensive hunting of the largest bulls, are not to be compared with the trophies that fell to the hunters of the 80s."

The Boone and Crockett "Records" will furnish American game managers a datum or bench mark from which they can measure the quality of stock as indicated by trophy size.

Criteria of a Satisfactory System. Hunting controls, after a long period of lopsided development, now seem to be entering upon a period of rapid change. No one can predict the outcome, but it is possible to set down some of the criteria which new systems should meet if they are to be an improvement over the present one. (The plural, "systems," is used deliberately, because it seems improbable that any one system can fit the growing diversity of biological, economic, and social set-ups.)

The American Game Policy (1930) asserts that, first of all, the private landowner must be given some incentive, more powerful and more universal than altruism, for controlling hunting and game environment on his land. His control of hunting must begin where legislative restrictions leave off. Given such an incentive, the following criteria are offered for judging workable controls:

1. The landowner's compensation for the hunting privilege should be in proportion to the size and quality of his game crop, so that he will have a personal incentive to improve the range and prevent overkilling, or other damage to the seed stock.
2. The landowner should, within the limits of the law, control who and how many persons are allowed to hunt on his land, so that responsibility for abuses can be fixed and the proposed total kill effectively limited.
3. The operating unit should be large and centrally managed, so that neither the sportsman nor the individual landowner will be burdened by the necessary routine of asking and giving permission to hunt. If possible, the minimum operating unit should be as large as the annual radius of the species.
4. Each operating unit should be responsible to the state for the condition of protected, non-game, and migratory species, for moderation in predator control, for law-observance, and for such other public interests as are involved. The state must retain the power to close the unit, or otherwise force the owners to care for the wild life which is its property.

As a necessary foundation for any sound system of hunting controls, each state should have:

1. Trespass laws making it illegal to hunt on enclosed, inhabited, or improved lands without the consent of the owner.

2. A system for examining license-applicants for fitness and responsibility, and for denying renewals of license to law-breakers.

3. A conservation department with sufficient stability and technical competence to be entrusted with large regulatory powers, and with sufficient funds to execute annual inspections of licensed projects. It must also have research service for answering the technical questions which are bound to arise from time to time.

Summary. Hunting is controlled by restrictions based on police power, incentives based on self-interest, and personal ethics.

Incentive controls are under-developed in this country, mainly by reason of non-recognition of the landholder as custodian of the state's game.

Restrictive controls are over-developed, in the sense that regulated incentives can accomplish simply what laws have failed to accomplish by elaboration of detailed prohibitions, namely, regulation of the kill to fit the productivity of each unit of range.

The technique of combining restrictive and incentive controls is growing rapidly. Success ratios and average bags are useful yardsticks for measuring hunting conditions. Shooting preserve laws and permit laws are being tried out as mechanisms for rewarding private enterprise in game management without relaxing protection of unmanaged areas.

Authority to regulate private enterprise implies technical competence in administrative agencies.

Control of hunting on public shooting grounds is still unsatisfactory.

Control of hunting is incomplete unless it recognizes and protects non-game wild life. Under some conditions it must also seek to reduce hunting accidents.

The American game policy lays down criteria for judging the soundness of systems for hunting controls.

This chapter, in the terminology of the philosopher, "does not make a complete circle." Its hiatuses reflect the chaotic status of actual practice.

We sportsmen are paying the piper for several decades of stagnation in the development of hunting controls. We have been fighting a rear-guard action for the very existence of sports afield. If we continue to regard the issue as a battle, we shall probably continue our retreat. But if we can see the issue as a mutual problem, confronting not only ourselves but also farmers, landowners, and protectionists, and soluble by their mutual cooperation, then a brighter outcome may be anticipated.

This hoped-for mutuality of effort cannot become a reality unless game managers know and understand other viewpoints, as well as their own. The protectionist's viewpoint is vigorously and ably set forth by Hornaday (1913, 1914, 1931). The landowner's experiences and attitudes are described by Lovejoy (1930).

An individualistic sportsman's viewpoint is depicted in story form by Lytle (1928), and in the form of a policy by Knapp (1930). Typical efforts to co-ordinate these conflicting views are those of Phillips (1931), the American Game Policy of 1930, and Leopold (1931*c*).

Chapter X

PREDATOR CONTROL

Attitudes and Policy. Predator control has received more attention than any other factor except hunting. This accords with the developmental sequence of ideas already explained in Chapter I.

Unfortunately, much of this attention, and many predator-control operations, have been based upon assumed or traditional predator-game relationships, or at best on generalizations supported only by a small number of observations which were, in the light of present knowledge, often misinterpreted.

Our knowledge of the inter-relationships of animals is still very imperfect, and current interpretations of evidence are doubtless still far short of the truth. It may be said with assurance, however, that they grow nearer correct as time goes on. The game manager is under obligation to be guided by the best available knowledge in his predator-control policies, else the standing of his profession, and the welfare of the game, may both suffer.

Predatory animals directly affect four kinds of people: (1) agriculturists, (2) game managers and sportsmen, (3) students of natural history, (4) the fur industry. There is a certain degree of natural and inevitable conflict of interest among these groups. Each tends to assume that its interest is paramount. Some students of natural history want no predator control at all, while many hunters and farmers want as much as they can get up to complete eradication. Both extremes are biologically unsound and in many cases economically impossible. The real question is one of determining and practicing such kind and degree of control as comes nearest serving the interests of all four groups in the long run.

This assertion is no mere paraphrase of the "happy medium." The actual conflict of interest is not nearly so great as the several factions suppose. The complexity of the game-predator relationship is greater than any of the four groups suppose. In spite of this complexity, however, the actual measurement of losses from predators is thoroughly feasible, as proved by such work as

Stoddard's. As these measurements progress, the apparent conflict of interest is being continually whittled down and reduced to specific local issues, or sometimes even to no issue at all. Common sense usually suggests a way to act on these local issues, whereas in their generalized form the same issues appear to be in irreconcilable conflict.

This chapter will attempt to picture as clearly as possible a mechanism of depredation, and to isolate as many as possible of its known working parts for separate examination. In order to keep our minds focused on the thing being isolated, the endless succession of ifs and ands which might be raised concerning its workings in special cases will be deliberately omitted. We are not referees to a controversy; we are trying to gain an insight into a complex phenomenon. We are not trying to render a judgment, but rather to qualify our minds to comprehend the meaning of evidence.

What Determines Loss from Predators? Subject to the physical adaptations of each, the annual direct mortality from predators in a given species of game on a given range depends on five variables:

1. The density of the game population.
2. The density of the predator population.

(1 and 2 determine the game : predator abundance ratio.)

3. The predilection of the predator, that is, his natural food preferences.
4. The physical condition of the game and the escape facilities available to it.
5. The abundance of "buffers" or alternative foods for the predator.

(5 in comparison with 1 determines the relative abundance of various kinds of prey.)

The whole predator-game relationship constitutes a biological equation in which the predator must balance his predilections (3) against the difficulty of satisfying them (1, 2, 4, 5). It should not be overlooked that this difficulty decreases as the game density goes up under management.

It is also usually true that escape facilities commonly deteriorate with intensive agriculture.

The last two variables in the equation (4, 5) fluctuate violently with weather for reasons which will be explained later. In the case of migratory predators, the second variable likewise fluctuates greatly as between years.

There are many indirect losses and gains from predators, some of which will be mentioned later.

Standards for Measuring Loss. Losses from predators on any unit of range may be measured in three ways:

1. The number of head of game killed by an *individual* predator during a unit time.
2. The total number of head of game killed by the predatory *species* during a unit time.
3. The *percentage* of the game population killed by the predatory *species* during a unit time.

Any statement of fact or policy on predator control must specify on which measurement it is founded, in order to be clear, and sometimes in order to be true.

Research work on predator food habits has so far adhered largely to the first standard, the unit time being indeterminate but varying from a few hours (stomach contents) to many days (pellet analysis).

The third standard is the most pertinent to game management, but the hardest to apply. It will be used unless otherwise specified in the following discussions.

Some predator losses pertain to nests rather than head of game. The third standard, in the form of percentage of observed nests destroyed by predators, is the only usable yardstick for nests. In renesting birds, however, the number of nests observed in a season is not the same as the number of nesting hens, even though all the nests be found. It is greater by the percentage of renestings, which is so far unknown for any species in any locality. This is discussed in Chapter XV.

Abundance Tables. The ideal starting point for considering the five variables determining predator mortality in any given locality would be an "abundance table" comparing the densities, or populations per unit area, of all species found in that locality. Such a table Elton (1927) calls "the pyramid of numbers." A complete pyramid of numbers does not yet exist for any locality in the world, but the observant game manager can often quickly patch together a rough idea of the density of those species with which he is most concerned, as of their critical season. Table 29 gives an example, partly consisting of mere estimates, of the "pyramid" for gambel and scaled quail range in southern Arizona.

TABLE 29

ABUNDANCE TABLE

Santa Rita Range Reserve, Arizona

Breeding Populations on 1 Square Mile

	Number	Species	Basis
	1	Coyote	Rough estimate
	2	Horned Owl	" "
	2	Redtail Hawk	" "
	10	Blacktail Jackrabbit	Strip count
	15	Hognosed Skunk Spotted Skunk	Rough estimate
	20	Roadrunners	" "
	25	Cattle (over 1 year old)	Forest Service Permits
	25	Scaled Quail	Rough estimate
	25	Cottontails	" "
	45	Allen's Jackrabbit	Strip count
	75	Gambel Quail	Rough estimate
25,628	1,260	Kangaroo Rat (Dipodomys)	Taylor, W. P. "Methods of Determining Rodent Pressure." Ecology, Vol. XI, No. 3, July 1930, pp. 523-542.
	6,400	Wood Rats (Neotoma)	
	17,948	Mice, spermophiles, and other rodents	

Game: Predator Ratios. Table 29 indicates that on this particular range there are, at the beginning of the breeding season:

25 quail for each raptor.
100 quail for each coyote.
7 quail for each skunk.
5 quail for each roadrunner.

In Missouri the *Game Survey* (p. 224) found that during the winter season the quail : fox ratio presented the following extremes of variation as between counties:

1,500 quail for each fox in Ripley County.
75 quail for each fox in Franklin County.

We have here a variability of over 2000 per cent in the game: predator ratio within a given state due to the differing density of the predator alone. (There is no great difference between the two counties in the density of quail.) If we arbitrarily assume that in Ripley County each fox caught a quail per day throughout the year, the annual mortality from foxes would be only 24 per cent. On the other hand, in Franklin County the same rate of depredation would exterminate the entire quail population in a little over two months. Obviously the assumption is arbitrary (there is no information on what quail depredations foxes commit in this state), but it is nevertheless clear that the game : predator ratio is often just as important in determining the percentage of predator mortality, and possibly more important, than the predilections of the predator. If the quail depredations by foxes under a given density of quail are anywhere near constant, it could safely be said that in the first case fox losses might be disregarded, whereas in the second case quail management would be impossible without radical fox-control measures.

In California, Boone (1928), quoting Jay Bruce, estimates that typical deer range contains one cougar per township. He does not give a deer density, but assuming 10 per square mile (half the Stanislaus density) the ratio would be:

360 deer for each lion.

T. C. West (unpublished), Assistant Supervisor of the Sequoia National Forest in California, found three lions using an exclusive range of 60 square miles. Assuming the same density of deer as above, the ratio would be:

200 deer for each lion.

Franklin Schmidt (unpublished) found from winter tracks in the defunct drainage districts of Wood County, Wisconsin, about:

1 prairie chicken for each weasel.

Skunks, foxes, and coyotes were very much scarcer.

None of these ratios are vouched for as accurate, but they could hardly be so inaccurate as to invalidate the general conclusion that a given species of game, in relation to a given predator, may be anywhere from one to a thousand times as numerous as its enemy.

This disparity in relative abundance certainly affects the question of whether the depredations of that enemy can be tolerated, and probably affects the predator's disposition or ability to commit them. On the latter question, more will be said later. On the former, it may here be said that any "blacklist" or "proscription list" advocating the killing of certain predaceous species must always be subject to the proviso "if the species is numerous enough, in relation to the game, to enable it to do material harm."

Effects of Density. The previous caption has considered only the variations in relative abundance of prey and predator. We have now to consider the effects of variation in absolute abundance, or density, of prey and predator.

It is obvious that the same game : predator ratio may obtain for high and low densities of each. Thus in Table 29 we have a quail : raptor ratio of 25 : 1 under a density of

1 quail per 6.4 acres.
1 raptor per 106 acres.

But we might encounter the same 25 : 1 ratio of relative abundance under an absolute abundance or density of

1 quail per acre.
1 raptor per 25 acres.

Under which condition would the percentage of annual mortality in quail be the greater? We of course do not know, but it would probably be greater under the greater density. The greater "fruitfulness" of hunting a unit acreage would probably more than offset the greater competition between predators for hunting ground. For reasons to be pointed out later under "Resistance," this would probably be more true of the percentage of nest and juvenile mortality than of mortality in adult quail. In fact, the percentage of mortality might rise with rising density of game even if the density of raptors did not rise, because in such cases there would be no additional competition.

On the other hand, if the density of quail decreased, the percentage of annual mortality, even under a stationary density of predators, would probably decrease because of the lesser fruitfulness of hunting a unit acreage.

Increasing density of game is, of course, the typical situation on a range where game management is being inaugurated. An accompanying increase of predators is normally to be expected, partly by reason of the increased food supply offered by the game as such, partly by change in predator habits, partly by reason of "buffer" species attracted by game food, and partly by reason of influx of migratory and mobile species of predators. The game manager should normally expect that the percentage of loss in game obtaining previous to management will, in the absence of control measures, increase as management progresses. On the other hand, control measures may reduce the loss. In any event a measurement of loss previous to management does not necessarily remain dependable later.

Specific measurement of skunk depredation on quail nests under a condition of increasing quail density due to management and decreasing skunk density due to control work was made in Georgia by Stoddard (p. 189):

YEAR	NESTS STUDIED	PER CENT OF NESTS DESTROYED BY SKUNKS
1924	59	25.5%
1925	104	16.5%
1926	85	10.5%
1927	354	7.0%

In this instance, control measures evidently reduced the loss, in spite of a rising density of quail.

McAtee (1932, p. 144) after an exhaustive analysis of the species of animal food found in 80,000 bird stomachs in relation to the probable abundance or availability of those species, concludes:

"Within size limits, animals of practically every kind accessible to birds are preyed upon, and as we consider the records for group after group a tendency for the number of captures to be in proportion to the abundance of the animal concerned is unmistakable. Availability is undoubtedly the chief factor involved in the choice of food, and predation therefore tends to be in proportion to population."

"*Buffers*." In the situation depicted by Table 29, we have as alternative foods for predators approximately:

1 rabbit for each quail.
250 smaller rodents for each quail.

These animals, averaging almost as large as a quail, are collectively more than 250 times as abundant as quail, and some species are easier for some predators to catch. It is obvious that in the aggregate they act as buffers to divert the attention of predators and satisfy their food requirements. This benefit is partially offset, however, by the fact that most of them compete with quail for food, while some of them (for instance, spermophiles) are themselves possibly predators on quail, in that they eat eggs and possibly chicks. There is still another possible offset to the beneficial effect of buffers: they may, provided they are more abundant than elsewhere, act as "bait" which induces an influx of mobile predators. Furthermore, some buffers harbor the diseases of game, and many the diseases of predators. Lastly hibernating buffers are unavailable to most predators during the winter, and nocturnal buffers are not available to diurnal predators, or vice versa.

This should suffice to make it clear that the exact effects of buffers on game are far too complex, too incompletely understood, and too variable from place to place to make possible any specific assertion for the guidance of game managers. By and large, however, it may safely be said that within the limits of the joint food supply, buffers are essential to survival of game. Their influence often extends beyond predators and food competition. They may even be responsible for fixing the vegetative type, and thus keeping the range habitable for game. Thus Farrow (1925) finds that in some English heaths, rabbits prevent the heather from being replaced by forest (which would render the heath non-habitable for red grouse). On the other hand, he found that too many rabbits cause the heather to be replaced by grass or bracken (both relatively worthless for red grouse food or cover).

Stoddard (p. 427) found that in Georgia the cotton rat has only a limited value as a buffer for quail. During the high year 1926 he determined that the cotton rat population in heavy broom sedge ran up to 40 per acre, whereas the quail population of the surrounding range, including moderate densities of broom sedge, never exceeded 1 per acre. The cotton rat, he found, directly competes with quail for pine seed, legumes, and other valuable quail foods, and in addition destroyed 3.5 per cent of the quail nests and attracted predators. Stoddard in this case considered these deleterious effects on quail as far outweighing the "buffer" service. The density of cotton rats, he thinks, is controlled primarily by the density of the sedge—one of many instances of interplay between the predator, food, and cover factors.

The classic example of "buffer" service is the snowshoe rabbit in its relation to ruffed grouse. Seton in his *Lives of Game Animals* (1929), gives an excellent life history, and in his *Arctic Prairies* (1923) much convincing testimony of the extent to which the northern predators depend on it for food, and their plight when the rabbits die off. Burnham (1918) suggested that the periodic scarcity of ruffed grouse in the north might be caused by depredations induced by the disappearance of this buffer food, and further south by the raptor migrations induced by rabbit scarcity. It now appears that grouse cycles occur even where migratory raptors do not (*Game Survey*, p. 139), but the buffer effect of snowshoes on grouse remains an unquestionable fact. There is less food competition between snowshoes and grouse than between cotton rats and quail, and no depredation, hence the former are a better illustration of buffer service. All cyclic buffers, however, tend to build up a heavy predator population which the game must sustain when the buffer dies off.

In weighing the influence of a given buffer on game depredation, one of the first things to consider is whether the buffer species in question hibernates. Hibernation produces each winter the same effect which the northern rabbit plague produces decennially—it throws upon the game the burden of sustaining a predator population which has fed all summer on buffers. It is equally fair to put it the other way: a buffer emerging from hibernation assumes a burden which the game has sustained all winter, and at a time when the breeding game may be especially vulnerable.

Errington has observed that a buffer temporarily covered by snow likewise throws upon other buffers, or game, the burden of sustaining predators. Thus in 1928–29 an abundance of mice sustained the foxes until deep snow came, after which they turned to rabbits, the mice being out of reach to the same degree as if hibernating.

By and large, the net benefits of buffer species seem to accrue when they are plentiful enough to make profitable hunting for predators, but not so plentiful as to eat up the food, act as bait to predator influx, or prey on game themselves. All buffers have a very high breeding potential, and many possess a catholic appetite for a wide variety of foods. Over-control of predators may bring about an excessive increase of buffers, which, unless checked by disease or artificial poisoning operations, may seriously injure the range and hence the game. Farrow ascribes the excessive abundance of rabbits on English heaths to over-zealous predator control by gamekeepers.

Artificial poisoning is often an unsatisfactory remedy because of its cost and the danger to game, livestock, and beneficial wild life. (See both Linsdale, 1931, and Kellogg, 1931.)

It is not to be supposed, of course, that every increase of buffers is due to predator control, or that the cessation of predator control would necessarily insure a desirable level of density in the species which form their prey. Enough has been said in Chapter III to indicate the extreme complexity of density phenomena, and the danger of fallacy in rule-of-thumb diagnosis.

Harassment. One adverse effect of predators, apparently not heretofore recognized as important, occurs when predators prevent game from feeding, or otherwise interrupt its normal routine, by confining it to "escape coverts" or other safe but often foodless places. Even though no actual mortality be suffered, such harassment may have serious indirect effects, especially during critical seasons. Thus during the short days of northern winter when food is scarce, and continuous search for food necessary to keep "body and soul" together, the confinement of a covey of quail by a hawk for hours at a time may effectively start that cumulative deficit of input over output which constitutes starvation.

As already mentioned, Errington found that after harassment by a Cooper's hawk, a quail covey may entirely change its previous feeding place, and remain confined to dense "escape coverts," not only during the hawk's visit, but for a week afterward. If there be no food within such coverts, the covey must either starve and freeze, or venture forth and be progressively picked off.

The Game Survey (pp. 73–74) found that during the hard winter of 1929–30, most of the quail coveys visited in Missouri were being harassed by hawks, including species probably incapable of catching any but weakened birds. The frequency of evidences of killing by hawks appeared to be inverse to the sufficiency of escape cover (usually osage) at the covey headquarters, and to the food therein (natural, or artificially supplied). The tracks showed the daily cruising radius of each harassed covey to be surprisingly short (often under 50 yards), and usually co-extensive with the escape coverts. All of the visible evidence pointed to the conclusion that harassment of foodless coveys led to their subsequent starvation, or decimation by hawks of some kind, whereas harassment of fed coveys did no visible harm. It was not determined what species of hawks were responsible for the frequent evidences of "murder" which were found, but this question is irrelevant to the present contention that there is an intimate relationship between harassment, cover, food, and winter survival, and that one of the most effective forms of "predator-control" is plenty of escape cover and food.

We do not know how the intensity or duration of fear in quail varies as between the slow and fast species of hawks, or with the vigorous or weak condition of the quail themselves. Errington has many instances which suggest a large difference between their fear of Cooper's hawks, marsh hawks, and redtails, the fearsome behavior seeming to decrease in intensity and especially duration in the order named. It may be that harassment by a redtail does not even prevent feeding. These details are in need of more light.

Harassment is not confined to game birds and raptors. I have seen coyotes calmly attending does with fawn, evidently watching for one moment of relaxed vigilance on the part of the mother. It is obvious that the doe cannot feed herself or nurse her offspring in a normal manner while thus attended. Knowles (1928) watched coyotes undertake a more spirited harassment of doeantelopes with hidden fawns. A small degree of such harassment is probably beneficial in keeping the game "on its toes," but a large degree is certainly not conducive to productivity. It seems obvious that high game density and a low predator density is conducive to limited or beneficial harassment, the predator moving on when unsuccessful in dealing with a vigilant and vigorous individual or group, whereas a low game density and a high predator density is conducive to unlimited and probably harmful harassment. It would seem that the selective or sanitary effect would be greater in the former case.

Inter-Predator Relationships. We must now consider the depredations of predators on each other. The subject is just beginning to unfold, so that only a suggestive sketch will be attempted.

Pennsylvania, famous (or notorious, as you will) for her former hawk and owl bounties, has also paid bounties on weasels. The annual "yield" of weasels presented for bounty appears to be going up, as follows:

1915–20,	average	36,794	per year.
1920–25,	"	49,029	" "
1925–30,	"	54,707	" "

Has this any connection with the generally admitted fact that the larger hawks and owls are going down? The horned owl is known to prey on weasels.

Mutual depredations between crows and horned owls are known to exist. The owls catch crows on the roost, and the crows eat owl eggs.

Small owls are eaten by large ones, particularly long-eared owls by horned owls. The frequency of screech owls in suburbs probably reflects the absence of their enemy, the horned owl. This is one more reason why a high density of horned owls on a game range is undesirable.

On the other hand Errington has evidence of a horned owl killing an adult Cooper's hawk on at least one occasion, also less complete evidence of a horned owl cleaning up a brood of Cooper's hawk nestlings.

Errington has noticed that in the region of Dane County, Wisconsin, Norway rats seem to become established in a wild state only where cornshocks are abundant and horned owls are absent or scarce. He suspects that the owls control this pest, which in Britain is known to be one of the worst predators on game birds.

A horned owl making away with a half-grown housecat which it had evidently killed was captured by Austin (1932, p. 33). Errington found a mink skull in the summer pellet of a horned owl.

Eaton (1931) finds indications that since 1925 Accipiterine hawks in New Jersey increased 14 per cent, while the larger hawks decreased up to 54 per cent. It is possible that the really harmful Accipiters are "filling the gaps" in relatively harmless hawks created by uninformed hawk-shooters in the name of "conservation."

This caption does not either condemn or exonerate any species for the behavior here noted. These are isolated instances which suggest that inter-depredation is one of the important variables in the ecological equation, but which do not establish a value for it in any case. This caption is aimed at shallow-thinking extremists who see in the whole predator issue nothing more than a question of "soft-heartedness."

The Rôles of Skill, Accident, Fitness and Education. In order effectively to appraise or predict game-predator relationships, the game manager must understand the rôles of skill and accident, respectively, in bringing about situations in which mortality can occur, the importance of fitness for a successful escape, and the effective "education" which fit game derives from a successful escape.

There is little doubt that some depredations occur through fortuitous meetings of predator and game, the frequency of which depends on the laws of chance alone.

On the other hand, depredations may be clearly the result of an exercise of hunting skill by the predator, and escape the result of the skill or fitness of the game. It is probably common for first encounters to be fortuitous, and for subsequent encounters to result from deliberate hunting, the outcome depending on the skill acquired accidentally on both sides.

Types of Depredations. There are three typical combinations of accident, skill and education. The first is where small recurrent losses are the result of accident alone. Thus Errington (1931*a*) missed a bobwhite or two from each of several coveys located near nesting horned owls, and recovered their remains from the current owl pellets, or from the nest, or both. No other losses from owls had been found in these coveys, except a very few during the winter. It is improbable that a horned owl ordinarily finds it profitable to look for the nearly invisible roosting coveys on the ground, but in the intensive hunting around the owl nest accident will doubtless make available an occasional bird night-flushed by mammals, or some bird late in joining the roost. Such accidentally available birds succumb, but their death is not followed by any change in the owl's ability to repeat the performance, or the quail's ability to prevent it. Its repetition remains a matter of pure chance. The aggregate number of deaths increases with the density of either prey or predator, but the percentage of annual mortality only with the density of the predator. This type of depredation may be called "chance depredation."

On the other hand, Stoddard believes that when a coon or skunk finds, by accident, a series of quail nests, he develops the ability to find more, and becomes an habitual egg-eater, provided he finds nests often enough to reward his effort. Such depredation, under a condition of heavy or increasing density of prey, such as accompanies management, is cumulative. While the predator develops increasing skill, the prey probably does not develop increasing resistance, except as his density may dwindle, or he may gradually cease nesting in the predator's habitat. This type of depredation may be called, for short, "habit depredation." Its characteristics are that both the aggregate number and the annual percentage of deaths increase with increasing prey density, while both probably decrease with decreasing prey density.

Decreasing predator density (such as accompanies predator control) decreases the annual percentage of deaths. An actual measurement of this decrease was made by Stoddard, and is summarized under "Effects of Density."

The third type of depredation was first clearly described by Errington (1931*c*). He found that a Cooper's hawk, in preying on a bobwhite covey in Wisconsin in winter, usually killed a bird per day for one, two, or at the most three days after arrival. By this time the covey ceased feeding in the open, often changing its menu entirely, and made such skillful use of escape coverts as to avert further losses. The Cooper's hawk persisted for a few days in his unsuccessful attempts, and then moved on "to pastures new." The modified behavior of the quail persisted to an extent suggesting the supposition that they were henceforth nearly hawk-proof, provided, of course, food supplies held out.

This type of depredation calls for mobile predators moving successively from one group of "green" prey to another. In the impolite but expressive vernacular of slang, it may be designated as the "sucker list" type. Its characteristic is that the prey "bites only once," thereafter building up an effective "sales resistance," but the predator continues his "nefarious" livelihood by virtue of the new and unsophisticated coveys which are "born every minute."

The per cent of annual mortality from this type of depredation would seem to rise with predator density only up to the point where all the coveys become "educated." This point would represent a fixed maximum beyond which few additional losses would occur. The aggregate deaths might increase with either prey or predator increase, but not the percentage. It is conceivable that the "education" presumably arising from this type is, in the long run, a net benefit to the game, *provided the escape coverts and food are varied and ample* (see Errington, 1930).

This brings us to the fourth and fifth types of depredation, which arise from some weakness in the prey or its environment.

The "education" of the "sucker list," for instance, is of no avail if there be not ample escape coverts, and abundant alternative foods of high quality, available during the weather prevalent at the time of attack. Without an environment which remains favorable even at the critical season, the result is not education but annihilation. There is no sanitary or educational recompense for such loss. It is commonly the precursor of starvation, and for lack of a more comprehensive short label may be called the "starvation type." The per cent of mortality in this type obviously increases with the density of predators, is probably not much affected by the density of the prey, but is affected by many extraneous and temporary variables such as weather. Its control should be a prime objective of management. The prime control measures are food and cover.

The fifth or "sanitary type" of depredation consists of the culling of diseased, crippled, or "dumb" individuals, often by predator species too clumsy to cope with normal healthy game.

Errington (1931*a*) believes the depredations of Buteo hawks on Wisconsin bobwhite are of this type, and Stoddard (p. 206) holds the same belief for Georgia. Errington suspects that diseased rodents likewise tend to be eliminated by the slower hawks. No level-headed game manager will regard this culling process as anything but beneficial.

These types, of course, overlap each other under varying circumstances. They are here set off as separate categories for the purpose of helping the game manager think intelligently on the predator problem. There are doubtless other types equally distinct, but as yet unrecognized. Table 30 summarizes their characters.

TABLE 30

TYPES OF DEPREDATION

Type	Selective?	Benefit	Damage	Principal Characteristic
1. Chance	No	None	Usually small	Stays small
2. Habit	No	None	May be large	Grows with management
3. "Sucker list"	No	Education	Limited	Bad if food and cover lacking
4. Starvation	No?	None	May be large	Often follows No. 3
5. Sanitary	Yes	Elimination of unfit	Small	Entirely beneficial to game

Selective Predator Mortality, Sanitation. Many of the controversies between sportsmen and biologists arise from a fundamental difference in viewpoint as to the significance of mortality from predators.

McLean (1930*a*) gives the biologist's viewpoint in a nutshell when he says:

"There is a growing tendency on the part of scientists to defend the predator as indispensable to the welfare of the animal preyed upon."

By "indispensable" is meant, I suppose, that continuous culling of weak or unfit individuals by which evolution has adapted our present species to their respective environments. This is a long-time viewpoint. It fears the degeneration of game stocks, and the elimination of predators as an esthetically valuable part of the fauna. It predicts unexpected and possibly dangerous reactions from too stringent control measures.

A coherent epitome of the opposite point of view is not so easy to find. Jack Miner (1931) gives the viewpoint of many sportsmen when he says:

> "At the present time there are many weak-hearted indoor naturalists who would lead one to believe that you shouldn't even kill a bedbug. . . . Birds are an open book. . . . Who wants to protect a creature like the weasel or the crow, when personal experience and knowledge compel one to believe that a crow will feed its young from fifty to one hundred innocent birds' eggs in one day, if he can find them?"

This quotation is selected because Jack Miner raises the real issue when he asserts: "Birds are an open book." Are they? If so, then the whole "progress" of ecological science for the last century is a pipe-dream.

The sportsman's usual attitude may be fairly termed a short-time viewpoint. He fears that growing game-scarcity may result in the ultimate prohibition of hunting, and sees in predator-control a "stay of execution." All too often he is unaware of what biologists are thinking about when they challenge his policies.

Phillips (1931) gives a viewpoint which may be quoted as a fair example of those sportsmen and game managers who try to understand both biology and sport. He says:

> "Sportsmen must be made to understand many things. They must look at all wild life in a broader way. It is foolish for their journals to tell them that they can have abundant game if only they will exterminate predatory birds or something of that sort. We know they cannot. The only way to handle this delicate question . . . is to protect all species . . . with two or three exceptions, except when they are doing or about to do damage. Sportsmen should discourage the destruction of hawks for sport alone, but at the same time leave the farmer or game breeder absolutely free to protect his own property."

This present issue in predator-control policy is, in its abstract generalized form, a seemingly hopeless impasse. But when research splits it up into its component local fractions, it becomes steadily less formidable. The latest life-history studies, as interpreted in the preceding caption, tend to show that the selective mortality or sanitary culling effect which the biologists wish to perpetuate *is operative in only certain types of* depredation, which can usually be tied down to particular species, seasons, and circumstances. They tend to show that the *heaviest game losses often occur from types of depredation in which the least culling occurs, and from species already condemned* by many biologists, and admitted by them to be in no danger of extermination. They tend to show that *culling losses can often be tolerated by game management*, at least in the lower grades of intensity.

Leopold (*Game Methods*, 1931*c*) argues that the higher scales of intensity are unnecessary in this country because of the low human population density, and that high-intensity management would be poor economics and poor esthetics.

Probably the most valuable recent advance in this process of splitting up the predator problem is Errington's thesis that better food and cover represent, in many instances, the cheapest and most effective predator-insurance.

In short, more game research, moderate game management, and mutual patience appear to be the most hopeful keys to sound predator control, and the ultimate reconciliation of biology and sport.

Predators and Game Distribution. Racial sanitation by culling the unfit, and controlling other predators of more destructive habit than their own, are not necessarily the only benefits which the game manager derives from predators, and which help offset the toll they take of game. There are probably other effects which as yet defy definition, much less explanation. It is said that a normally distributed herd of deer on Vancouver Island, after the lions and wolves had been killed off for their benefit, suddenly "huddled up" on a small part of their original range and overgrazed it. Apparently normal depredation had some as yet obscure influence in keeping the deer normally distributed over the range. In this case there is no assurance that the control work and the huddling were actually cause and effect. The case is cited merely as suggestive of many possible predator influences as yet beyond our vision.

Odd and New Predators. Stoddard's discovery already described in Chapter II, that the fire ant is an important destroyer of pipped quail eggs just about to hatch, indicates that the list of predators affecting the productivity of particular game species is not yet complete. He also found occasional quail nests broken up

TABLE 31A

PUBLICATIONS ON PREDATOR FOOD HABITS*

(Compiled in collaboration with W. L. McAtee, U. S. Biological Survey)

Species	Author	Date	Locality
General	Forbush	1916b	Massachusetts
Bobcat	Criddle	1923	Manitoba
		1925	Canada
	Dixon	1925	California
	Poole	1929	California
Coyote	Criddle	1925	Canada
	Dixon	1925	California
	Poole	1928	California
	Henderson	1930	General
	Hall	1931	Western
Cougar	Dixon	1925	California
Crow	Barrows & Schwarz	1895	General
	Barrows	1912	General
	Kalmbach	1918	General
		1920	"
		1920a	"
		1920b	"
	Sanborn et al	1919	Oklahoma
Domestic Cat	Forbush	1916a	New England
	Wilson & Vreeland	1917	N. Y. and N. J.
	Gabrielson	1922	Western
Fox	Crosman	1927	New England?
	Errington	1932a	Wisconsin
Hawks & Owls	Fisher	1895	General
		1907	"
	McAtee & Beal	1912	General
	Gloyd	1925	Kansas
	Preble	1927	General
	Hausman	1927	New Jersey

Species	Author	Date	Locality
Hawks & Owls	Gross	1927 1928a	General
	Brooks	1928 1929a 1929b 1930	General and S.W. Canada
	Bird	1929	Manitoba
	McAtee & Stoddard	1930	General
	Errington	1950 1930a 1932	Wisconsin " "
	Baldwin et al.	1932	Ohio
Magpie	Day	1927	Wyoming
	Kalmbach	1927	West
Skunk	Dixon	1925	California
	Hamilton	1929	East
	Corsan	1930	Michigan
	Williams	1930	General
	Dearborn	1932	Michigan
Snakes	Guthrie	1932	General
Roadrunner	Gorsuch	1932	Arizona

*For full reference see Bibliography.

by wild turkeys. A comparable case is the recent disclosure that reindeer eat duck eggs. Yeatter (1932) found a Hungarian partridge nest which had been broken up by domestic chickens. Errington saw a chicken kill a quail chick. More thorough life-history research will doubtless reveal many more special predatory relationships, some of which will be important enough to warrant control.

The invasion of northern latitudes and high altitudes by coyotes means, in effect, a new predator as yet but inadequately studied in its new range. The northward spread of the crow into the Canadian wheat-belt, and the invasion of California and the southern Lake States by the opossum, are additional evidence that an unending series of new and puzzling situations are to be the price of our dominion over the earth.

Predilection; Food-Habits Research. The preceding discussions will enable the game manager better to understand both the value and the limitations of the scientific data so far available for his guidance in questions of predator control. These data, obtained through the activities of the Division of Food Habits Research of the U. S. Biological Survey, and of other research ornithologists and mammalogists, usually reach us in the form of composite averages of thousands of individual analyses of stomach contents or pellet contents for each particular predatory species. Raptors and crows have been much more thoroughly reported than the predatory mammals. Adult mortality has been much more thoroughly reported than juvenile or nest mortality. Fisher, McAtee and Beal, and Barrows may be referred to as examples of this early foundational work.

This composite average is commonly but incorrectly interpreted as representing the fixed food preference, predilection, or habit of the species in question. It is commonly but incorrectly inferred that the food habits of that species will conform roughly to the composite pattern at most particular times and places.

If the reader has correctly understood the foregoing discussions he will not need to be told that this is hardly true. He will understand that these composite patterns are the average of a vast number of local and temporary situations, in each of which all the variables which we have just been discussing have come into play. While the species will run true to pattern in many or even a majority of instances, and while the general "good" or "bad" character arrived at through such general food-habits research will hold good in almost all of them, it nevertheless remains true that in some cases radical departures from the pattern are to be expected. In short, composite averages are merely the starting point for the game manager's job of getting local facts.

The process of getting dependable local facts about mammals as well as raptors, and on juvenile and nest as well as adult mortality, is thoroughly feasible. Stoddard has set the example of what these local measurements should be, how to make them, and how to use them in practical management operations. The recent findings of Errington, Gross (1930*a* and *b*), Wight (1930), and others show how Stoddard's technique for localized studies is rapidly spreading into the other states.

A list of publications on the food habits of important predatory groups appears in Table 31*a* (pp. 248–249). This has been compiled through the courtesy of Doctor W. L. McAtee of the

TABLE 31B

PUBLICATIONS ON CONTROL TECHNIQUE*

Species	Author	Date	Locality
Bobcat	Young	1931	General
Coyotes & Wolves	Carhart & Young	1928	Colorado
	Young	1930	General
English Sparrows	Kalmbach	1930b	General
Feral Cats	Forbush	1916a	Eastern States
	Silver & Jarvis	1929-30	General
Magpies	Kalmbach	1927	West
Rats	Silver	1930	General
Mammals	Bailey	1932	General
General Controls on Game Farms	McAtee	1927	General
Finance and Organization, 10-year program	Jardine	1929	General
Effect of Pole Traps	Wight	1931b	Michigan

* For full reference see Bibliography.

U. S. Biological Survey. The detailed reference for each publication listed appears in the general bibliography in the appendix.

Table 31*b* is a list of publications on control technique for important predatory groups and certain other species.

Summary. Predator loss in game is determined by density of game and predator, predilection, escape facilities, and buffer species. Per cent depredation usually goes up with game density, by reason of increasing fruitfulness of a unit of effort. It usually goes down with increase in buffers, subject to certain disturbing influences such as predator-influx, buffer hibernation, and buffer cycles.

Harassment by predators may affect game welfare or induce starvation over and above any actual killing.

Predators prey on each other to a much greater extent than is usually supposed. Some species, by controlling others, are a benefit to game.

There are five types of depredation, each offering a different balance between the desirable culling of the unfit and the undesirable decimation of the game stand. The improvement of cover and food is a better protective measure against some types than the killing of the predator.

Composite studies of predator food habits are only a general guide to local problems.

This ends our inadequate attempt to interpret the great invisible drama of tooth and claw in which the sportsman plays a lead, though he has neither seen nor read more than snatches of the other parts. If he emerges from this review with the idea that the whole play is hopelessly complex, he will have missed the point. If on the other hand he feels his curiosity intrigued and his fairness challenged to gain a better understanding of his local problems, then our purpose is accomplished. There is only one completely futile attitude on predators: that the issue is merely one of courage to protect one's own interests, and that all doubters and protestants are merely chicken-hearted.

Epicurus wisely observed: "It is impossible but that those who are feared by many should themselves be in continual fear of some." If the sportsman will ponder this well, he may get the point: to reserve his "courage" until he has determined as closely as possible where his own interests lie.

CHAPTER XI

CONTROL OF FOOD AND WATER

Interaction of Factors. The previous chapters have shown that all of the factors of productivity are interwoven, and react upon each other as well as upon the game whenever there is a change in any one of them. This interaction is especially pronounced as between food, water, coverts, and special factors. In actual management their control is all one problem.

It is also a noteworthy fact that in actual management, deficiencies in food and cover are often seasonal rather than yearlong. The practical problem of control is usually a matter of providing the kind, amount, and distribution of each which experience indicates will suffice for the species in hand at its critical season.

Game Physiology Unknown. Experience, however, tells us little or nothing about *why* certain foods are eaten or rejected, or what rôle the various foods play in sustenance or reproduction of the species. Even the most scientific food-habits research tells us *what* has been eaten, but not always how much, and never for what reason.

The physiology of wild animals is almost entirely unknown. A few game species are closely related to domesticated animals in which the physiology of nutrition has been studied to a limited extent, but these studies have been largely empirical rather than scientific, and have stressed weight rather than fitness. Some of the most important game species, such as the budding grouse with their obviously specialized digestive powers, have no relatives in captivity, for the reason that captives are not yet successfully bred. Antlered game has no domestic counterpart except reindeer. Hence analogy with the food requirements of domestic species is seldom possible.

Control of game food, water, and special factors under such a limited understanding of game physiology is necessarily an empirical art, in which predictions are never wholly safe, classifications of phenomena are more or less arbitrary, and we know what much oftener than we know why. All of this chapter is subject to this unavoidable limitation.

An exploration of wild-bird physiology has now been begun by the Baldwin Bird Research Laboratory of Gates Mills, Ohio, but no game birds have as yet been studied.

FOOD

Definition. A game food, in the sense used in management, is any material which is ingested by game for the maintenance of productivity.

Control of the food factor implies the control of the kind, quantity, and quality of food needed by any given species, at various ages and seasons, in a given environment.

Variety of Game Food. An understanding of food control must begin with an appreciation of the tremendous variety of foods eaten by most game species. Game eats a greater variety of species than humans do, the lack of Frigidaires to the contrary notwithstanding.

Stoddard found in 1659 Georgia bobwhites nearly a thousand kinds of food, of which several hundred occurred with sufficient frequency to suggest they were important.

TABLE 32

KINDS OF FOOD FOUND IN 1659 BOBWHITES BY STODDARD

CLASS OF FOOD	NUMBER OF KINDS OF FOOD (p. 509)	IMPORTANT KINDS OF PLANT FOODS (p. 541)
Seeds	112	25
Legumes	68	24
Cultivated plants other than legumes	11	12
Grass seeds	66	8
Sedge seeds	26	2
Mast	18	4
Spurge seeds	16	2
Fruits	55	19
Green vegetation	44	11
Insects	500	?
Other animals	11	?
	927	107

The two columns are not exactly comparable, the left column consisting of species and the right partly of genera. If this were corrected, and if important insect foods were included, the total number of important food species for quail would doubtless exceed 200.

The red grouse has possibly the simplest dietary of any game bird. It feeds on 30 plants, plus an unknown number of insects (*Grouse Report*, p. 83).

The Hungarian partridge seems to have the simplest dietary of any American game bird. Kelso (1932) found 46 plants and 34 animals in 80 partridges from the central states and Washington.

Gross (1930) found 93 plants and 99 animals in 39 pinnated and sharptail grouse in Wisconsin.

He found (1928*b*) 123 plants and 117 animals in 390 ruffed grouse from various states, of which 58 occurred in 10 or more birds.

Gorsuch (1932) in the month of August 1930 alone found 114 species of plant and animal food in 30 stomachs of gambel quail in Arizona.

The same diversity holds good for game mammals. Todd (1927) found cottontails eating 71 shrubs and trees in a single small locality during one winter season. Clepper (1931) records 113 woody plants browsed by Pennsylvania deer. In both rabbits and deer the number of herbs eaten is doubtless at least as great as the woody plants. Robinson (1931) found deer in the Sierras eating 80 browse plants, 61 weeds and herbs, and 28 grasses and grass-like plants, total 169 items.

Elements of Selectivity. Obviously the game manager cannot control 1000 or even 200 species of plant and animal food. He will do well if he controls half a dozen. Their skillful selection requires some orderly understanding of what determines the kinds of food eaten or needed by game. As nearly as is known, the kinds of food eaten are limited by:

1. What is present at the season in question.
2. What is available or accessible without undue work or exposure.
3. What is palatable in kind or condition.
4. What is needed for current physiological processes.
5. Habit. What the individual is accustomed to eat, and skilled in finding.

The first limitation needs no comment. There are no mulberries present in January, and no buds or corn in July.

The other limitations need elaboration.

Availability. Stoddard has pointed out that a seed falling into a thick mat of pine needles is not available to quail. The work necessary to find it is excessive and unprofitable, especially when the same seed is obtainable elsewhere on bare ground.

Errington suspects that locust seeds encased in the pod on the tree cannot be gathered by quail without an expenditure of energy (in flying into the tree and clipping the seeds) greater than its food value.

Foods buried under snow or sleet are obviously not available except to a limited extent for species which scratch or burrow. Browse on limbs or branches higher than a deer can reach by standing on his hind legs is not available. Hence the "Plimsoll Line" on woody vegetation (Burnham, 1928) and the earlier starvation of yearlings because they cannot reach browse at the higher levels accessible to grown deer.

An unhusked ear of corn is not available to quail until the quail has learned by slow degrees how to clip the husk away. A cornshock in the middle of an open field watched by a Cooper's hawk is not available to game in the nearby covert.

It is thus evident that physical availability may depend upon the level at which food occurs, the degree to which access is obstructed by mechanical obstacles, the risks run in reaching it, and the stage of "education" of the individual game animal.

Palatability. It seems improbable that birds "taste" the many foods inclosed in non-soluble coatings, which they nevertheless eat with avidity. Palatability, therefore, cannot be a matter of taste alone. It seems probable that a comfortable degree of engorgement of the crop, and a feeling of welfare as digestion begins in the gizzard, enter into the obvious preferences shown as between foods. It is also quite certain that the size of the food unit, in reference to the convenience of finding and swallowing it, enters into that selectiveness which we call "palatability."

Grange thinks that color may possibly help determine palatability. Cornfield-using mallards in northern Iowa avoid fields of white corn, as distinguished from yellow. This, of course, does not prove the point.

Any scale of palatability is obscured by variations in availability and in season. Thus we cannot compare the palatability of grasshoppers with that of poplar buds to pinnated grouse, because the two foods are not present at the same season. Neither can we compare locust beans in a tree to ragweed seeds at a convenient level for quail to reach, because the latter are so much more accessible. It is also possible that many foods which are accessible and of a convenient size are shunned because either instinct or experience has shown them to have toxic qualities.

Palatability likewise has seasonal variations distinct from accessibility or presence. Thus Stoddard found that cherry-pits become palatable after they begin to sprout in spring. The change is doubtless chemical, as well as physical (in the sense of splitting of the hard shell in germination).

Again Dixon (1928) found that Yosemite deer use deer brush (*Ceanothus integerrimus*) as a staple food in winter, but do not eat it at all in summer. Some change, either in the constituents of this shrub, or in the needs of the deer, is doubtless responsible.

Special Physiological Needs. Despite our ignorance of game physiology, it may be safely said that food selectivity is sometimes guided by the need of special food for the support of current physiological processes. Both the *Grouse Report* and Stoddard observe that hens gain in weight more rapidly than cocks just previous to the breeding season. Later studies may show a difference between the sexes in the amount or kind of food eaten at this period. The specialized feeding resorted to by poultrymen to induce egg laying strongly corroborates this assumption. Schmidt (unpublished) observes that on the approach of cold weather, sharptails begin budding even where provided with an abundance of grain, of which they continue to eat in moderate quantity. Under the same conditions pinnated grouse do not begin to bud until spring. The current physiological need of resisting cold, coupled with differences in digestive powers, may have something to do with this unexplained difference in food behavior between two outwardly similar species.

Habit; Relation to Exotic Foods. The recent trend of research strongly suggests that game must learn by experience how to eat exotic foods, and possibly some native foods also.

Stoddard (p. 125) found that Georgia quail unaccustomed to buckwheat or rice took several years to learn to eat them, although the former occupies a high place in the palatability scale for most game birds, after the habit has been formed.

Bogardus (1847) asserts that pinnated grouse had to learn to use corn as food and cover, and that the habit was not formed until years after corn became common on the Illinois prairies.

Errington (1931*a*) finds that the ability of bobwhite quail to clip the husks from corn ears is not an instinctive, but distinctly an acquired characteristic or aptitude. Some individuals, he suspects, may never learn the trick.

Schmidt (unpublished) observed that sharptail grouse, eating buckwheat from hoppers at Wisconsin feeding stations, did not recognize husked ears of corn, laid on the ground near the hopper, as a food. They soon learned to eat it, however, and later how to scratch the husks from unhusked ears, provided a few grains were exposed. Coveys not previously introduced to corn refused to enter traps baited with husked ears, whereas other corn-wise coveys entered at once. Two sharptails attached to a large covey of pinnated grouse knew how to eat corn from the outset, having evidently acquired the "art" from their relatives.

Gorsuch (unpublished) found grain to be useless as bait for trapping gambel quail in the non-agricultural brushfields of Arizona. "These birds have no conception of what grain is. . . . I have on numerous occasions watched them wade through grain for several days before one would venture to take a piece." After about three weeks of baiting a given covey would learn that grain was good to eat, after which the trap would be set and the birds successfully caught for banding.

The contradictory evidence on whether ruffed grouse eat grain may reflect actual differences in previous access to grain, and corresponding differences in the grain-eating habit.

One may safely deduce from the foregoing evidence that experience, training, or habit is a fundamental element in food selectivity, and that the most accessible and palatable of foods may be of no avail until the game has formed the habit of eating it.

A large proportion of our (now) most valuable game foods are of exotic origin. All of the grains except corn, most of the agricultural weeds, and many of the legumes and grass seeds which now form the backbone of the preferred and staple foods for small game, are exotics, and their utilization presumably an acquired character.

Classes of "Sustenance" Foods. Experience teaches us that the diet of game animals, through the critical winter season, often follows a more or less definite sequence. As one group of foods becomes exhausted or unavailable, a second group is taken, and as the second becomes exhausted, a third is taken. These groups presumably represent a descending order of palatability, although it is by no means certain that seasonal changes in physiological needs do not also enter the equation.

In fall, after the foods characteristic of summer have disappeared, the foods eaten and seemingly preferred for as long as they last into the winter, may tentatively be called *preferred foods* or delicacies. For example: neither bobwhite nor pinnated grouse consumes corn in quantity until ragweed seed becomes scarce. Mule deer in the Southwest eat no Juniper berries until pinon nuts or mesquite beans have become scarce.

The group of foods resorted to after the supply of preferred foods has dwindled may be called *staple foods* because they are the foundation of winter sustenance. Game which has plenty of staple foods maintains full weight and vitality, and winters with small loss.

It may possibly be that some staples, such as corn for bobwhite, are rejected in early fall, not so much because they are less palatable than preferred foods, but because the physiological need for them does not develop until cold weather. Lesser palatability, however, is for the present the simpler and hence the preferable explanation.

The group resorted to when staple foods become scarce may be called *emergency foods*. Locust beans, for example, are not sought by quail until corn is scarce. These emergency foods may be defined as capable of sustaining life, but as a sole ration they often do not suffice to maintain weight, vitality, and resistance over prolonged periods of adverse weather. They may suffice, however, when mixed with a small quantity of staple foods. Some emergency foods may be somewhat toxic.

Starving game, in the absence of better food, often fills up on material of little or no nutritive value, which may be called "*stuffing*," because it seems to be eaten simply to fill the digestive organs. Errington's experiments with quail (1931*b*), for example, indicate that on a sole diet of sumac, wild grape, or rose hips, quail lost 6–8 grams per day, whereas they lost 14 grams on no food at all. This does not prove, of course, that such foods lack value when mixed with, let us say, corn.

Table 33 presents some tentative examples of the four classes of winter food. It should be understood that in most species, food habits research is still too sketchy and too local to permit of a final classification of palatability, and furthermore that the items in any one class for one species are simply estimated to be of similar palatability to those appearing in the same class for another species. Thus Schmidt (see table) is quite sure that pinnated grouse in central Wisconsin eat corn earlier in the winter than sharptail grouse do, but some other investigator in some other place might find corn equally palatable to both, or he might push both up one place on the scale, and call corn a preferred food for pinnated and a staple for sharptail. It should also be understood that the table ignores possible seasonal changes in physiological needs. It is based entirely on the sequence of observed changes in consumption.

There appears to be a fifth class of food. Dixon (unpublished) has pointed out that deer consume small quantities of a large variety of browse plants, in a manner and to an extent which suggests analogy with the chewing of gum, grass blades, bits of wood or stems of leaves by human beings. Such consumption evidently represents nervousness, or exercise for the teeth, or *pastime*, as distinguished from consumption by reason of hunger. Stoddard likewise found a large variety of materials in quail crops which are hard to account for as foods in the ordinary sense. These miscellaneous ingestions may be called *pastime foods*. They doubtless account for part of the difference in the sums of the two columns in Table 32.

The seasonal sequence of foods which has been sketched qualitatively in this caption, is also visible in quantitative classifications of stomach contents. Fig. 24, showing a classification of pheasant food by months, is taken from *The China Pheasant in Oregon* (unpublished), 1929.

Variety. It is not to be supposed that the palatability-sequence postulated in Table 33 and described in the foregoing captions is a complete and fully established theorem which explains all game-food phenomena. It is merely a preliminary attempt at the orderly interpretation of what to me at least has seemed a chaotic accumulation of facts. It does not explain all of those facts.

Thus wild game birds have been known to eat *some* dry corn in the middle of summer, and *some* emergency foods or even

Table 33

PALATABILITY SEQUENCE OF WINTER FOODS

Class	Species and Examples of Food in Each Class						
	BOBWHITE (Stoddard)	S.T.GROUSE (Schmidt)	PIN.GROUSE (Judd, Gross & Schmidt)	WILD TURKEY (Stoddard & Judd)	W.T.DEER (Lovejoy)	MULE DEER (Leopold)	COTTONTAIL (Wight & Todd)
PREFERRED FOODS	Trefoil Ragweed	Buckwheat	Buckwheat Oats Barley Ragweed	Chufas	Apple ?	Pinon nuts Mesquite beans	Sumac bark & sapwood Raspberry twigs Blackberry twigs
STAPLE FOODS	Grains Japan clover Acorns Pigeon grass seed	Birch buds Aspen buds	Smartweed Corn	Corn Acorns Beechnuts	White cedar	Cliff rose Mt.mahogany Ceanothus Ariz. Oak Juniper berries Aspen browse	Apple twigs Basswood twigs Locust twigs & pods Many others
EMERGENCY FOODS	Locust beans Sweet clover seed Buckbrush berries ? (Symphoricarpos)	Corn	Poplar buds Birch buds Elm buds Maple buds Willow buds Sumac berries ?	?	Hemlock	Juniper browse Gambel oak ?	Conifers ?
"STUFFING"	Sumac berries Rose hips	?		?	Balsam ? Laurel leaves & twigs Rhododendron buds	Pinon browse White fir Douglas fir	?

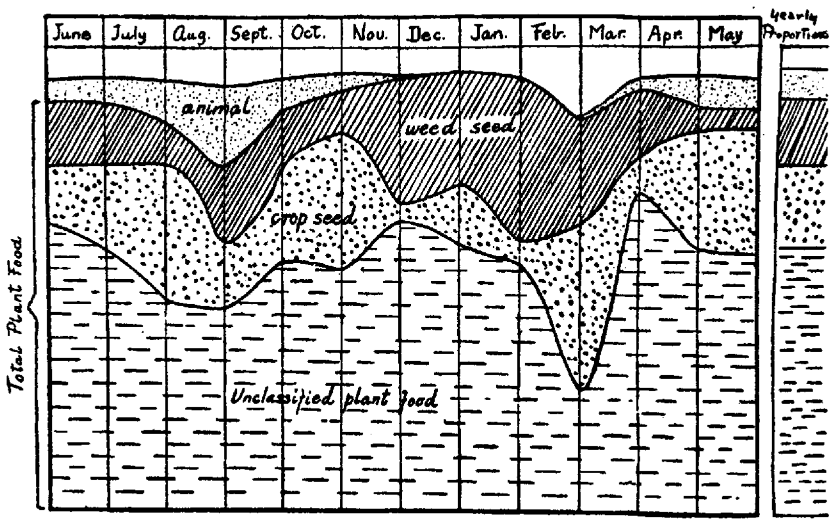
stuffing in the presence of a surfeit of delicacies. A preference for variety, the inertia of habit carrying over from previous months, and the principle of pastime, or idle pecking at whatever falls under the eye, jointly or severally, doubtless account for the minor degrees of non-conformity to this palatability scale which are known to occur.

FIG. 24

CLASSIFICATION OF PHEASANT FOOD BY MONTHS

Food of the adult pheasant showing varying proportions of each by bulk from month to month, and the relative proportion of each in the aggregate annual food based upon the examination of the contents of 139 stomachs.

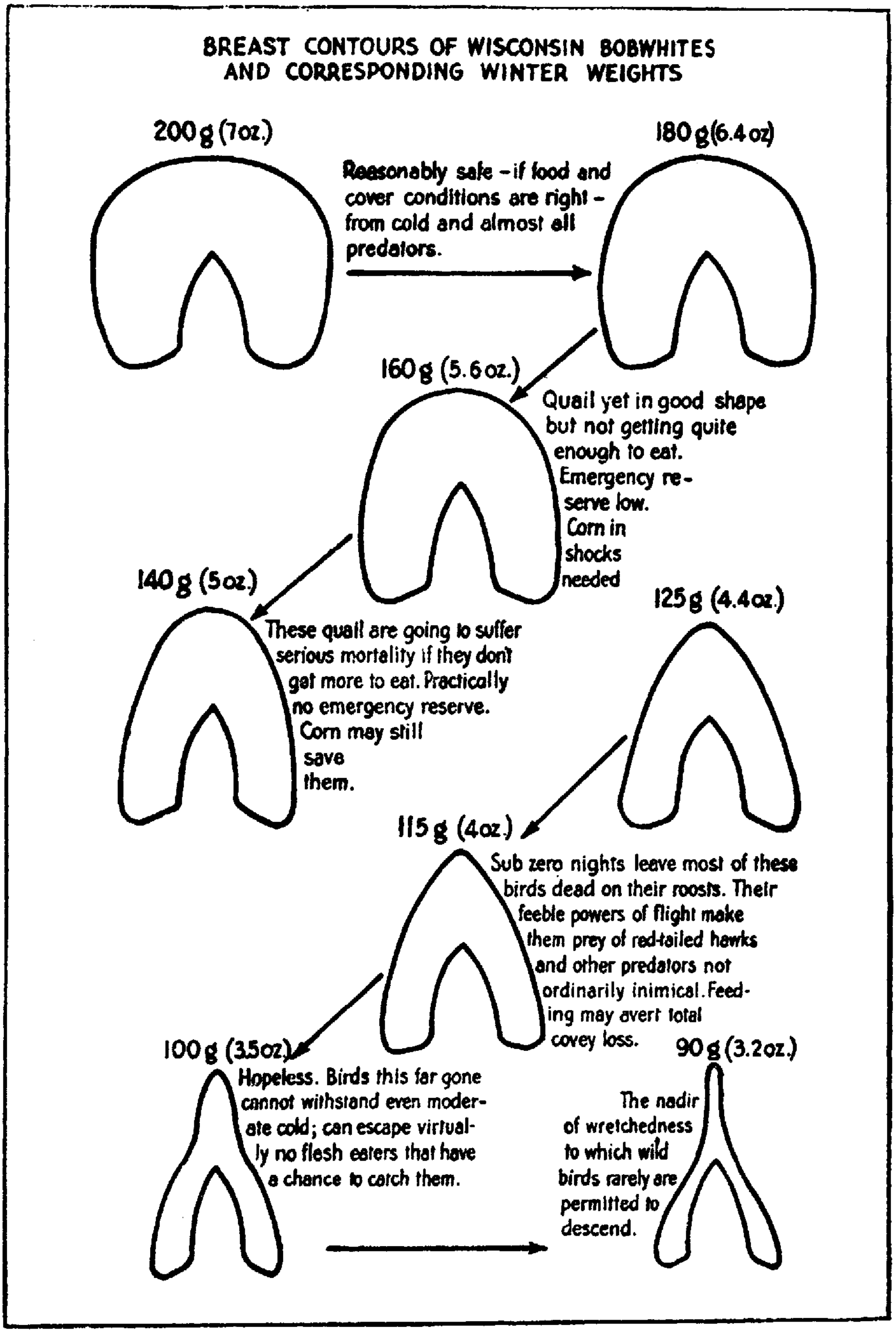
(Reproduced by courtesy of Oregon Agricultural Experiment Station)



Starvation. The availability-sequence from preferred food through staples and emergency foods to worthless "stuffing" is paralleled by a corresponding decline in the physical condition of the bird which Errington (1931*b*) has depicted for bobwhite in a series of typical weights and breast contours shown in Fig. 25.

Sudden deprivation, however, will kill bobwhites long before they reach the bottom of Errington's scale. Four to six foodless days will kill a fat quail in cold weather. Gradual deprivation of

Fig. 25


BREAST CONTOURS OF WISCONSIN BOBWHITES AND CORRESPONDING WINTER WEIGHTS
200 g (7 oz.)
180 g (6.4 oz)
Reasonably safe – if food and cover conditions are right – from cold and almost all predators.
160 g (5.6 oz.)
Quail yet in good shape but not getting quite enough to eat. Emergency reserve low. Corn in shocks needed
140 g (5 oz.)
These quail are going to suffer serious mortality if they don't get more to eat. Practically no emergency reserve. Corn may still save them.
125 g (4.4 oz.)
115 g (4 oz.)
Sub zero nights leave most of these birds dead on their roosts. Their feeble powers of flight make them prey of red-tailed hawks and other predators not ordinarily inimical. Feeding may avert total covey loss.
100 g (3.5 oz.)
Hopeless. Birds this far gone cannot withstand even moderate cold; can escape virtually no flesh eaters that have a chance to catch them.
90 g (3.2 oz.)
The nadir of wretchedness to which wild birds rarely are permitted to descend.

200-gram Wisconsin birds renders them a prey to slow hawks at 130 grams.

"Below 120 grams (4.2 ounces) . . . quail in the wild are as good as done for."

A bird is still alive at 90 grams—Errington's *Nadir of Wretchedness*—only by virtue of an exceptional combination of protracted mild weather and absence of predators.

The *Game Survey* (p. 58) shows a limited number of weights indicating that Missouri quail starved during the hard weather of 1929–30 at 3½–4½ ounces. This checks with Errington's critical weight of 4.2 ounces.

The bearing of these data is obvious: The game manager can build up, probably for any species of game, a series of weight-criteria which can be used to judge the condition of his stock, and warn him of impending starvation.

The physiology of starvation involves not only deficient nutrition, but depressed body temperature. The maintenance of body temperature under varying conditions of food and cold is being investigated by Baldwin and Kendeigh of the Baldwin Bird Research Laboratory (1932). This investigation is of great import to management.

Grit. Most of the literature on game foods recognizes only two functions of food: (1) sustenance in the ordinary sense of maintaining weight, vitality, and resistance, and (2) mechanical action on other foods. Grit for birds is the familiar example of the second function. All of the preceding discussion has dealt with the first function.

Few laymen realize the power of a gizzard armed with grits. Many are astonished when assured that a dainty quail can grind whole corn. Let them marvel, then, at McAtee's account of what happens when a mallard eats hickory nuts (1918, p. 7):

"These hard nuts might be thought beyond the powers of a duck to digest, but, on the contrary, they are taken care of with ease, being broken by the great pressure exerted by the gizzard as they are on the point of entering that organ. Once wholly within they quickly are ground to fine fragments."

Information on the mechanical function of food is accumulating rapidly, but it is doubtful whether our interpretation of it is as yet very profound.

Only two lines of investigation have so far been begun: (1) the amount of grit found in birds, and (2) the peculiar ability of some species to conserve their grits when new supplies are cut off. In England a limited comparison of preferences as between various minerals has also been made.

The quantity of grit found in game birds is given by various authors as follows:

TABLE 34

WEIGHT AND VOLUME OF GRIT IN BIRDS

	Weight of Grit in Gizzard and Crop	Per Cent of Food in Crop (Volume)
Pinnated grouse (Gross, 1930)	1.5 grams	6
Sharptail grouse (Gross, 1930)	0.3 grams	2
Ruffed grouse (McAtee, unpubl.)	?	3
Bobwhite (Stoddard, p. 123)	?	1-3 (max. 14)
Red grouse (Grouse Report, p. 95)	7.8 grams	?
Hungarian partridge (Kelso, 1932)	?	40 (max. 90)
Pheasant (Cottam, unpubl.)	?	26
Mallard (McAtee, unpubl.)	?	13
Canvasback (McAtee, unpubl.)	?	19

These quantities do not, of course, show the rate of ingestion, nor do they show all the more soluble minerals which may be eaten and promptly ground up and absorbed.

Stoddard (p. 123) found the amount of grit in bobwhites to be so variable that he gives no average figure. The amount, he says, decreases when hard seeds, such as those of loblolly pine or wild cherry, are being eaten in quantity. By contrast with bobwhite, the *Grouse Report* (p. 95) states that the amount of grit in red grouse is nearly constant. Cock grouse (and cock pheasants) contain more and larger grits than hens, and adults larger and more polished grits than the young. Quartz is preferred, and was found even in birds living on range devoid of quartz. It was inferred that these birds had either flown across a wide valley to get it, or had extracted it from watercourses which had transported it from adjacent areas. Quartz is artificially supplied to some grouse moors as a management measure. "This expedient has met with some success, but has not been very extensively adopted. The artificial introduction of quartz grit has frequently been tried with pheasants, and always with success."

The astonishing grit-content of Kelso's Hungarian partridges cannot be dismissed as exceptional, since it is the average of 80 birds from three or four states and all months of the year. I formerly entertained the thought that grouse, with their ability to squeeze nourishment out of a vast bulk of buds and other coarse vegetable foods, probably carried the most grit. That thought is now dismissed. No wonder Hungarians show such a strong tendency to seek gravel in the wake of snowplows (*Game Survey*, p. 121).

Most game birds, as may be inferred from Table 34, eat grit daily, pheasants and doves particularly frequenting gravelled roads at nightfall, presumably for this purpose. Blue geese, where the feeding ground was distant from the grit supply, were observed by McIlhenney (1932, p. 290) to gravel every second or third day. Birds on concentration areas may occasionally consume grit in amounts of geological import: McIlhenney says a huge gathering of geese during the winter of 1930–31 consumed over a hundred tons of grit which he had put out for them.

When deprived of grit, certain birds are believed to conserve the supply on hand in their gizzards.

About all that can be said about conservation of grit is that there is such a thing, but it is not yet understood. Stoddard says of bobwhite:

> "When grit can be obtained easily, a portion of that in the gizzard is passed on daily, but when . . . the supply is cut off, that in the gizzard can be conserved for a week or more. The ability to conserve grit when it is scarce probably enables the birds to survive when . . . snow covers the ground for weeks."

Errington (1931*b*) found experimentally that bobwhites can conserve grit for at least six weeks. Six birds, after being fed a gritless ration for this period, lost only about 18 grams apiece, while the controls lost about 7 grams in weight. The gritless birds were, at the end of six weeks, not yet in danger of dying.

The *Grouse Report* (p. 97) says two red grouse were carried on a gritless ration for 21 days. The grits evacuated by normal birds were also washed out for measurement. The normal passage included up to 160 grits, but on cutting off the supply 116 were passed on the second day, and after that not to exceed 13. One of the two birds died on the 21st day. The Report suggests that the conservation of grit may be effected not so much by any selectivity of the gizzard in passing its contents to the intestine, but rather by a decrease in the amount of food eaten, and that grit starvation may actually be food starvation.

These findings carry less weight, however, than those of Errington and Stoddard, because of the lesser number of birds and the shorter duration of the experiment.

Some one should experiment with grit conservation in Hungarian partridge.

Grits and hard seeds are often found in the pellets of raptors. Such pellets are a good indicator of what gizzards and crops of prey the raptor has swallowed, or even its condition when caught. Errington (1932) made this deduction, which will show the point: An owl pellet was found to contain the skull of a quail. The other contents of the pellet included grits, showing that the crop had been eaten, and *sweet clover seed*, indicating that the quail was starving, and probably helpless, when caught by the owl (see Table 33). On the other hand grits and ragweed seed, or grits and corn, would have indicated an able-bodied victim.

Mineral, Vitamin, and Tonic Foods. The need of special foods to fill special physiological needs is not so far recognized in game, although it has long been recognized in cattle and poultry. It is probable that grit performs not only a mechanical function, but that the soluble parts of it may also be absorbed to fill some small but insistent need for mineral substances. As already pointed out, gallinaceous game as well as poultry can survive for a long time on a gritless ration, the grit already present being retained and used over and over again where ordinarily it would be passed out and replaced with new material. Nevertheless birds fed on such gritless ration consume grit eagerly when it is supplied. Possibly their residual grit suffices for mechanical purposes, but *not for the purposes of special nutrition* here under consideration.

It is well known in animal husbandry that many of the foods furnishing ordinary sustenance, likewise furnish vitamins necessary for growth, vigor, and reproduction. This suggests that there may be foods that furnish vitamins only, or minerals only, and which have no ordinary sustenance value. This still indeterminate group may be called *mineral and vitamin foods.* The characteristics of this group are that they may be dissociated from the ordinary functions of sustenance and mechanical grinding, that very small quantities may suffice, and that certain physiological processes may suffer if they are not supplied.

A nutritional hypothesis, premised upon the assumed need for special minerals or vitamins, was advanced by the *Game Survey* (p. 127) to account for the peculiar distribution of success and failure in plantings of pheasants and Hungarian partridges. As shown by Fig. 8 all southern plantings have failed, and success in the north is more or less spotty, especially in Hungarians. The grosser aspects of climate seem to be ruled out as a primary cause by reason of the known success of pheasants on game farms in the zone of failure, and by reason of the fact that failure of plantings is gradual, the planted stock at first breeding vigorously, but later "straggling" to an ultimate decline (see Table 8). Replenishment by new plantings, however, seems to renew the vigor of the stock, so that we have "artificial establishments" even as far south as Georgia. The grosser aspects of food, cover, predators, poaching and disease seem to be ruled out by reason of the consistent behavior of each species within its zone of success and failure respectively. These highly variable factors would, if controlling, produce a "shotgun" pattern of successes, whereas the actual pattern, especially with pheasants, is solid. Incidentally the zone of success for both species in the north central region lies mostly on glaciated soils, suggesting some connection with soil chemistry or associated plants. The zone of success for Hungarians lies within the zone for pheasants, but some spots (such as northeast Iowa) definitely show success with pheasants but failure with Hungarians.

These observed conditions would be satisfied if we postulate that each species requires certain minerals or vitamins, or different amounts of the same mineral or vitamin; that in confinement the requirements are usually met, regardless of where confined, by reason of the importation and mixture of artificial foods, but in the wild the requirements are met only where the soil or plants contain the needed substances. New plantings temporarily reinvigorate old stock in the zone of failure by the reserve stores contained in their tissues and communicated to offspring through the egg. Poultry researches show apparently parallel phenomena.

A seventh class of foods, which may be called tonic foods, consists of fruits and berries which most investigators find are consumed in large quantity by game birds, but which Errington's experiments indicate have little ordinary sustenance value. Stoddard (p. 235) quotes Nordhagen as suggesting that berries may act as an astringent and tend to prevent coccidiosis. The *Grouse Report* (p. 98) suggests that certain berries may act as a vermifuge, and that patches of berry plants should be fenced against sheep to increase the supply. In summer, fruits and berries are known to fill a water requirement.

It is probable that the need for certain mineral and tonic foods is not a continuing or constant need, but rather a variable one depending on what sustenance foods are being consumed. The mineral or tonic food may offset some injurious property in the sustenance food. Thus stockmen believe that range cattle require more salt while they are subsisting on oak browse. Possibly the high tannin content of the oak, or the large proportion of cellulose, accentuates the need for salt.

A new and seemingly parallel case has been discovered by Gorsuch (1932, unpublished) in the salt-eating propensities of gambel quail in Arizona:

> "During the winter of 1930–31 countless quail were seen eating the rock salt which cattlemen place about the waterholes. . . . This salt eating . . . is believed to be related to the cattle manure taken by the birds in scratching for mesquite beans passed by the cattle. In the winter of 1931–32 no instance of salt eating was found, nor were there any mesquite beans."

Possibly we may some day recognize a class of "offset foods."

The possible inter-relationship of the various functions or values of game foods, and their various degrees of palatability, is suggested in Table 35. It should be understood that this table is largely conjectural.

Poisonous Foods. The relation of wild animals to poisonous foods is at this moment so beset by conflicting evidence that no explanatory theory of poison losses can be advanced. It seems safe to say, however, that poisonous foods are usually nonpalatable, and hence that losses are usually small or absent, except where palatable foods are scarce.

TABLE 35

TENTATIVE CLASSIFICATION OF VALUES AND PALATABILITY IN GAME FOODS

	Class	Value for				Toxicity	Example
		Palatability	Sustenance	Special Nutrition	Mechanical		
Sustenance Foods	Preferred	high	high	?	none ?	none	Ragweed for bobwhite or pinnated grouse Buckwheat for sharp-tail
	Staple	medium	high	?	none ?	none	Corn for bobwhite
	Emergency	low	low ?	?	filling	some toxic ?	Locust or sweet clover for bobwhite
	Stuffing	low	almost none	?	filling or grinding ?	some toxic ?	Sumac seed for bobwhite
Other Foods	Pastime	?	none ?	none ?	none	none	Many misc. plants found in only small quantity in stomachs
	Tonic	high	low ?	high ?	none ?	none ?	Berries for bobwhite
	Mineral or Vitamin	high	none ?	high	high	none	Salt for deer Grit for gallinaceous birds

McAtee (letter, May 5, 1931) says:

"We doubt if there is anything resembling avoidance of poisonous foods by wild life. Animals either possess a degree of immunity to poisonous foods, or ordinarily take them in quantities too small to do damage when mixed with a mass of non-poisonous things. . . . The general rule regarding choice of food is that an animal takes whatever is most readily available, considering its size and degree of specialization in food habits. . . . If something deleterious happens to occupy this position, so much the worse for the animal, but ordinarily this does not happen in a state of nature."

It has sometimes been supposed that animals learn about poisonous foods when young, and are thus trained to avoid them. McAtee (1916) points out at least one case refuting this "training" theory: hundreds of pheasant chicks (also young ducks and chickens) on the New Jersey Game Farm died of eating rose beetles, which contain a neuro-toxin affecting the heart action of both chickens and rabbits. Chickens, however, became resistant with increasing age, and at ten weeks old were apparently immune.

The immunity of the older chickens is apparently the result of age rather than training. Whether pheasants likewise acquire an immunity with age was not determined.

Rose-chafers have the same poisonous effect on young poultry as rose-beetles.

Slautterback (unpublished MSS., 1930) reports the Pennsylvania Bureau of Animal Industry as finding that laurel (*Kalmia latifolia*) and rhododendron (*R. maximum*) are eaten by deer, especially in times of food shortage, but that these plants seem not to be poisonous to deer, although known to be so to cattle, sheep and human beings. Confined yearling deer starved into eating these plants in quantity exhibited symptoms of rickets and starvation, but not symptoms of poisoning.

Deer have been seen to eat loco, but no cases of injury, death or "loco-habit" have been reported in deer. Loco is possibly eaten only in small quantities for pastime, but this seems an improbable explanation. The fact that loco offers succulent greens in early spring when deer, from their inroads on alfalfa fields, are known to be avid for such food, taken in conjunction with the fact that no one has ever seen a "locoed" deer, is very strong circumstantial evidence that *some* protective mechanism exists, —either deer are immune to loco, or it is unpalatable to them, or they learn to avoid it. That exotic species like cattle and horses do *not* have the advantage of this protective mechanism, whatever it is, accords with what one would expect of the evolutionary processes of adaptation.

Dixon (1928), observing Yosemite deer through powerful glasses during their feeding hours, states that they seemed entirely to avoid larkspur, azalea, and cow parsnip, locally considered as poisonous to cattle and sheep.

While no general interpretation of the evidence on poisoning of wild life is as yet possible, the following fragments of an ultimate theory seem to hold water: (1) mammals have more highly developed organs for both taste and smell than birds, hence the avoidance of poisons through the educational effect of unpleasant individual experience is more probable in mammals than in birds; (2) exotic mammals sometimes succumb to poisons which native species on the same range either avoid, or eat without damage; (3) some birds seem immune as adults to poisons lethal in youth.

Quantities of Food Eaten. Nice (1910) found that captive bobwhites in Massachusetts consumed per day:

TABLE 36

FOOD : WEIGHT RATIO OF BOBWHITE

Season	Grams of Food Per Day			Approx. Wt. of Birds (grams)	Food: Weight (per cent)
	Weed Seeds	Insects	Total		
winter	(12–21) 15	0	15	170	9
summer (laying hen)	(? –24) 20	10	30	170	17
early fall (cock)	12	12	24	170	14

No other data on food-per-day : weight ratio are known to us. The ratio is of course not a measure of the actual nutrients ingested, since the moisture content of the food varies by seasons. Much of the summer intake of food is water.

Crop or stomach weights (meal : weight ratio) are more commonly recorded, but less significant. Table 37 gives some examples. The average full crop weighs around a half of the maximum engorgement. The number of times the crop is filled is not known, but a rough comparison between Stoddard's and Nice's figures would indicate less than twice daily for bobwhite.

Variable Composition of Foods. It is known that the chemical composition of a single kind of food, such as corn, varies according to the soil and climate in which it was produced. For this reason manufacturers of special prepared rations for poultry thoroughly mix their stocks of a given kind of grain obtained from various regions, before mixing it with other foods for distribution to consumers.

There is some evidence that similar variations occur in wild foods for game, and that these affect palatability and hence consumption.

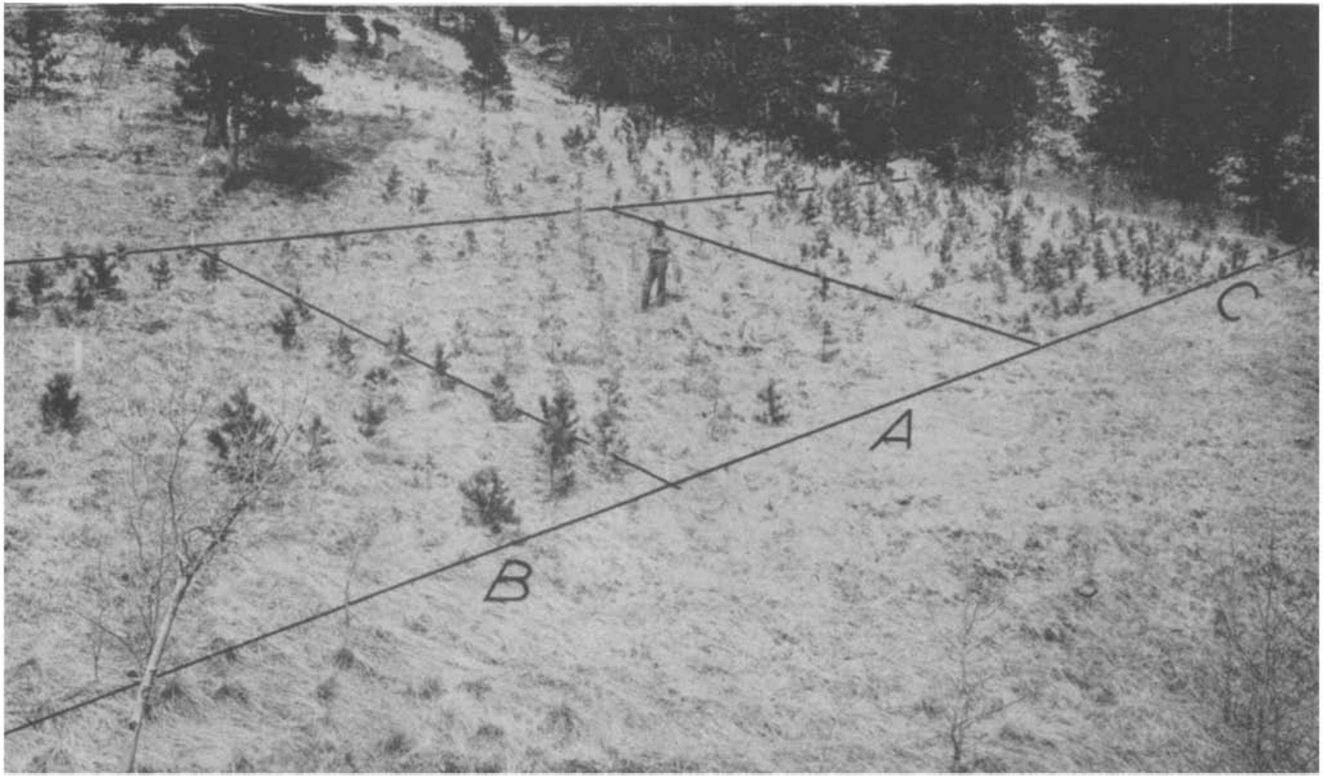


Fig. 26. Plantations at Freemont Forest Experiment Station, Colorado, showing how deer have distinguished in their browsing between western yellow pine of the same age but different origins. Plot *A* is pine from the Black Hills and has been almost consumed by deer. Plot *B*, partially browsed, is pine from the Leadville Forest. Plot *C*, unbrowsed, is pine from the San Isabel Forest. (Photo by C. G. Bates, formerly Director, Freemont Station.)

TABLE 37

CROP : WEIGHT RATIO

Species	Max. weight of crops	Average wt. of adult birds		Per cent of average weight of birds
		female	male	
Pinnated Grouse (Gross)	83	734	904	10
Sharptail Grouse (Gross)	35	717	827	5
Ruffed Grouse (Gross & King)	38	519	590	7
Red Grouse (Grouse Report)	39	590	650	7
Wild Turkey (1 bird only)	900		(9000)	10
Bobwhite Quail (Stoddard)	22	165	165	13

Thus Burnham (unpublished) asserts that balsam browse is a staple for deer in New York, whereas Lovejoy is equally confident that it is no more than a low-grade emergency food for deer in Michigan. Clepper (1931) lists it as only sparingly eaten in Pennsylvania.

Possibly regional differences in palatability of a given food are due to actual variation in geographic races of the food plant. Carlos Bates of the U. S. Forest Service reports a convincing instance of differing palatability when several geographic races are growing on the same spot (see Fig. 26). Several races of western yellow pine were planted at the same time in adjacent plots of similar soil, exposure, etc., on the Freemont Forest Experiment Station in Colorado. Local deer, browsing in the plots, showed a decided preference for the Black Hills race of pine. The most probable explanation is differing chemical composition. Thus Jeffrey pine, a variety of the Western Yellow pine, is commercially exploited for heptane, which is absent from the parent species (Mirov, 1929).

Other Determinants of Game Food. In addition to these variations in quality, and the obvious variations in kind and amount of game foods with soil and climate, we have now to discuss the variations in kind and distribution of game food brought about by industrial activities and by the competition of non-game species.

Agriculture, by the introduction of dozens of grains, forage plants and weeds, and by alteration of the native flora and fauna, has completely rebuilt the game food map of the continent (*Game Survey*, p. 59). Agriculture always changes and usually improves the game food supply, although the change may be so great as to necessitate the substitution of one species of game for another. Thus agriculture has almost excluded the prairie chicken from the cornbelt (*Game Survey*, p. 165), but farming in conjunction with fire and lumbering has extended the chicken range 300 miles northward into the coniferous forests of the Lake States. At the same time agriculture has admitted quail to the prairies formerly occupied by prairie chickens, and given quail a universal distribution in the adjoining woodland regions where in virgin times quail were either localized or absent.

In considering the effect of any industry on game food supply, one must take into account not only the primary operations which are purposeful and controlled, but also the tools and forces used to accomplish them which are commonly accidental and uncontrolled. Thus marsh fires are an uncontrolled tool of agriculture, and forest fires the unwelcome aftermath of lumbering. Drainage is a tool of agriculture, not quite uncontrolled, but nevertheless a powerful determinant of game foods. In fact marsh fires, forest fires, grazing, and drainage have profoundly changed game food, water, and coverts in many parts of the world, including nearly all civilized and all arid regions. Game management is possible only when these uncontrolled forces are either excluded, or subjected to control.

One of the most important determinants of game food, water, and coverts is the livestock industry. Here again we must deal not only with legitimate, stabilized animal husbandry, but also with the overgrazing which has accompanied unstable livestock operations on hundreds of millions of acres in the West, especially on the unregulated public domain. The damage done to game by overgrazing is little appreciated by the public in comparison with its appreciation of damage by fire and drainage.

This is because the deterioration of game food and coverts by overgrazing is qualitative rather than quantitative. Especially in semi-arid climates, overgrazing eliminates the palatable food plants without apparent reduction in the amount of plant cover. Worthless plants promptly fill in the gaps left by the valuable ones, and the layman sees no difference. To him the ruined countryside is still "beautiful." He suffers no pain over the invisible but fundamental deterioration which his own industries have inflicted.

The effects of fire, grazing, and drainage on game food and cover will be further discussed in the chapter on "Cover."

Lastly, game foods are determined by the competition of non-game species of wild life. Thus carp have more or less devegetated the choicest lakes, rivers, and marshlands on the continent. Jackrabbits, prairie dogs and other rodents consume a considerable part of the food plants available to game and livestock in the West. Cotton rats compete with quail for the same foods in the South. Rabbits keep the English heaths from reverting to forest, or by their own pressure force them back to grass or bracken. The general magnitude of the respective food-pressures of game and non-game animals may be inferred from the Abundance Table (Table 29) and the accompanying text.

Game as a Benefit to Agriculture. Ornithologists have for many years urged that game birds are beneficial to agriculture in consuming noxious weed seeds and insects, and that the farmer should for that reason encourage and conserve them.

As to insects, the most recent researches have fully sustained the original contention. They have also added convincing instances in which game *cover* has benefited agriculture by harboring songbirds and also *predatory insects* which serve as a check on insect pests. Thus Fluke (1928) finds that the pea aphid, one of the important enemies of the commercial pea crop, is less numerous in the vicinity of ungrazed woodlots, because such woodlots harbor predatory syrphid flies and lady beetles, which are the natural enemies of the pea aphid, and which keep it in check over a radius of 1/8 to 1/4 mile around each ungrazed woodlot.

As to weeds, the game manager cannot very consistently urge that game destroys weeds and at the same time urge leaving certain weeds at proper places as game food. Moreover, the trend of the recent evidence refutes the supposition that this year's weed crop depends on last year's seed, and the extent to which last year's seed was formed or consumed. In many weed species it seems rather to depend on whether physical conditions (weather, culture, shade, etc.) have encouraged or discouraged the germination or survival of seeds held in ground storage (see Stoddard, p. 390).

In short, the consumption of weed seeds by game birds probably has very little effect on the weed nuisance.

Winter Feeding Methods. Game is artificially fed in various ways. It is not the function of this text to describe detailed procedures, but rather to outline guiding principles. Detailed procedures are given in pamphlets by Conklin and Morton for Pennsylvania (1928), Pirnie for Michigan (1930), Schmidt for Wisconsin (1932), LeCompte for Maryland (1927), *Game Survey* (p. 72) for Missouri, and by McAtee for the U. S. Biological Survey in a regional series of Farmers' Bulletins (621, 760, 844, 912). Many papers (see Grange, 1931, and Errington, 1930) likewise deal with this subject.

For upland game birds all feeding methods fall into one or another of the following basic classes:

The Food Patch. An area or strip of grain left in the field, either uncut or shocked, for the winter use of game.

The Self-Feeding Station. A predetermined spot provided at long intervals with unhusked corn, a stack or pile of unthreshed grain, suspended bundles of unthreshed grain, hoppers of shelled grain, or other supplies so arranged as to "feed out" gradually, because not available without some effort on the part of the game.

The Feeding Station. A predetermined spot provided at short intervals with shelled grain or other "ready-to-eat" food. There is no effort required on the part of the game except to reach the station.

Emergency Feeding. There are no predetermined arrangements. The game is found after the emergency arises, and shelled grain or ear corn is put out at frequent intervals on the spot where found.

Each method has advantages and disadvantages which are more or less apparent from its definition.

The food patch must be installed in spring (or in fall if part of a field which is to be cropped anyhow), but requires little or no further attention during winter. There is risk of the patch being eaten out during the growing season by livestock or deer, or depleted prematurely in fall by stock, rodents, non-game birds, or the game itself.

The self-feeding station must be installed in fall, but during the winter requires replenishment only at long intervals. There is risk of the accessible grain becoming depleted between visits.

The feeding station should be installed in fall, and usually requires replenishment about every two days during severe weather. There is little risk of serious depletion by non-game animals.

Emergency feeding requires no advance preparation, but requires replenishment at least every two days. The risk is that the food may not be found by the game, and that the game may flush and scatter in the process of locating it, or during the frequent visits of the game manager.

All methods involve waste through consumption of food by rodents, and more or less risk of the food being covered by snow. Rodent wastage may be reduced by elevating the food above ground, or locating it a little away from thick cover.

All methods risk attracting predators to the feeding spot. Predators may harry the birds or confine them to refuge-cover, and thus prevent feeding, even though no game is actually caught. Such confinement is probably serious in short days of severe winter (see Chapter X). One partial preventive is to locate the station near ample cover, at a spot devoid of perches suitable for hawks. Another is to provide two or more stations for each covey, and so keep the predator "guessing."

The clumsier raptors, such as the red-tailed hawk, are sometimes useful at stations in preventing squirrels from carrying the grain away.

Emergency feeding is really suitable only for mild climates subject to severe but infrequent storms, and for species which winter in coveys or herds. It is not feasible to locate and feed individual animals after emergency weather sets in.

Feeding stations are suitable only for use near dwellings, or for people with ample time.

As nearly as is now known, it is advantageous to supply grit with all food for birds, especially where natural grit is deficient or covered up.

Food patches and self-feeding stations are superior under all conditions for all species subject to a real shortage of natural food. In the South, in places where natural food is very abundant, game may ignore even the best food patch (Stoddard, p. 378).

While it cannot be proved, I strongly suspect that a bushel of visible grain on the stalk, such as is presented in a food patch, will attract and hold more game than a bushel of invisible grain in the barn or in a hopper, no matter how promptly the latter is made available for emergencies.

In short, I suspect that visible feed in its "natural" state not only feeds but also holds game, whereas invisible feed artificially supplied at the eleventh hour merely prevents starvation of game which has found no better-looking place in which to winter. Moreover the food patch avoids the risk that the game may fail to find the food, or that the manager may fail to find the starving game.

To retard depletion in advance of emergency weather, the ideal food patch should offer both preferred and staple or emergency food. The preferred food will keep the game busy until the need for staple food is at hand. A corn patch, in which the last cultivation is omitted so as to enhance the growth of foxtail or ragweed, automatically assures this desirable sequence of consumption. The ragweed will hold the birds until the corn is needed. A combination of buckwheat and corn, or proso and corn, not only offers a palatability sequence but a maturity sequence. It not only assures a continuous food supply, but it tends to check wandering in both early and late fall. On the other hand a patch of straight buckwheat is liable, unless it is very large, to become exhausted before bad weather or scarcity of wild foods has begun. A proper sequence of foods in a food patch for pheasants is shown in Fig. 22.

Winter Feeding Characteristics of Species. The choice of a feeding technique involves something more than the choice of a food. The distance apart at which food patches are installed must fit the seasonal cruising radius of the species, whereas the distance apart at which emergency stations are placed must fit the daily radius, which is always shorter than the seasonal radius, and in cold weather is often very short. For example: a food patch visible throughout the fall might be found by quail raised a mile away, while an emergency station, installed at the identical spot but only after the onset of bad weather, might be missed by a covey located only a few hundred yards distant. The superior economy of the food patch is evident.

The aptitude of the species with respect to using a hopper, entering shelters, opening stacks, entering shocks, and clipping corn husks must likewise be known and allowed for.

Table 38 attempts to present these characteristics for various upland species. Their sequence of winter food has already appeared in Table 33.

Tractor Food Strips. A compact block or parcel of a grain field left uncut for game is not always the best food patch. Stoddard (p. 370), by running tractor plows through open woods, through heavy broom-sedge, and along fire-lanes, created long strips of food and thus increased the variety and interspersion of food and cover types over large areas. He found these long narrow strips more heavily used than the more compact patches.

Such strips need not necessarily be seeded to food-bearing plants. Under some conditions food-bearing weeds automatically follow the breaking of the sod, or the turning under of surface litter, and persist for several years. Stoddard often plowed successive halves of a long strip during alternate years, thus maintaining two different stages of plant succession, in addition to the third already present on the unplowed ground. The season at which strips are plowed often determines the kind of food plants which volunteer (Stoddard, p. 365).

The principle of diversification of food and cover by means of plowed strips is applicable wherever interspersion is insufficient (this is practically everywhere) and wherever power machinery can be used to tear up the soil. Modern tractors can tear up strips not only through old fields, but also light or scattered brush and open forests, and will doubtless prove important in grouse and deer management, as well as in quail management.

Summer Feeding. In the overcrowded pheasant coverts of England, grain and other staple foods are artificially provided during the summer months. In the more natural and less intensive type of game management hoped for in this country, summer feeding of staples is entirely unnecessary. Special provision for fruit, berries, and greens, however, is advisable wherever the natural supply is scanty.

For example, Stoddard (p. 382) found that mulberry trees could be advantageously planted on quail range, and were used by both young and old birds throughout the summer.

A strong growth of clover on old tote-roads, highway right-of-ways, and old clearings is confidently recommended as a profitable measure for grouse and deer management. Light cattle grazing, periodical cultivation, and clearing away of heavy shade may in some cases be necessary to make the clover thrive. The desirable clovers will not thrive on light soil. Some soils require inoculation for clover.

Wild strawberries provide both greens and berries for ruffed grouse, and can be encouraged by periodical cultivation and removal of shade.

Sheep sorrel is an important source of greens for sharptail and prairie-chicken. (Schmidt, unpublished.)

Where forest-fire control has made sufficient progress actually to reduce the frequency of fires, the wild-berry crop may decline. Intolerance of shade and other competition causes berries to follow fire. The same properties may be utilized to induce a berry crop without wholesale burning. For instance, the burning of segregated brush piles on cutting areas, and the tearing up of fire lines with tractors, will bring in berries just as effectively as a wholesale burn.

Aquatic Foods. Management of waterfowl often involves the control of aquatic food plants and other vegetation. Moose and deer during the summer season likewise feed on aquatics to a considerable extent. There is an enormous literature on aquatic botany, but a rather meagre one on the culture and control of aquatic game foods. Table 39 provided by McAtee gives leading American references.

The food habits of aquatic feeders, to the extent that they are known, can be derived from the literature cited in Table 40, Publications on Game Food Habits.

Game Food Habits Research. Space prevents any review of the available information on food habits of each game species. The literature has developed along substantially the same sequence as that already mentioned under predator food-habits research: the early publications gave composite cross-sections of food habits for the country as a whole, whereas more recent publications describe local studies which differentiate between seasons and between varying local conditions.

Table 38

WINTER FEEDING CHARACTERISTICS OF UPLAND GAME BIRDS

Species Authority Locality	Effective Radius of Station (Miles)		Will use hopper?	Will enter roofed shelter?	Will strip tight husks from corn ear?	Will open stacks of small grain?	Will penetrate loose corn shocks?
	Daily*	Seasonal[x]					
Bobwhite (P. L. Errington, Wis.)	0.2	1.0 ?	yes?	yes	yes, learn by experience	no	yes
Pheasant (H. M. Wight, Mich.)	0.3	2.0 ?	yes	yes	yes	yes	yes
Hungarian Partridge (R. E. Yeatter, Mich.)	0.2			no		no	no
Pinnated Grouse (F. J. W. Schmidt, Wis.)	2.0	large	no	no	yes	no	no
Sharptail Grouse (F. J. W. Schmidt, Wis.)	0.5	2.0	yes	yes	yes, learn by experience	no	no
Ruffed Grouse (R. T. King, Minn.)	0.2 ?	1.0 ?	?	yes	?	?	?
Cottontail	0.2 ?	?	yes	yes	yes	yes ?	yes ?

* The daily wanderings of birds located at station.

x The distance from which birds are likely to come in search of a winter location. Depends largely on whether previously fed in same place.

TABLE 39

PUBLICATIONS ON AQUATIC GAME FOODS

Subject	Author	Date	Locality
Background of Agriculture	Needham & Lloyd	1916	General
Propagation of Wild Duck Foods	McAtee	1911b 1914 1915 1917	General
	Mickle & Thomson	1913	Ontario
	Pearce & Terrill	1920	General
	Titcomb	1923	General
Surveys of Wild Duck Foods	McAtee	1917	Missouri
	McAtee	1920	Nebraska
	Metcalf	1931	North Dakota
	Mickle & Thomson	1913	Ontario
	Wetmore	1921	Utah
Wild Rice	Chambliss	1922	General
	Mackie	1930	California

Table 40 lists some of the more important references for some of the more important species or groups.

By and large, food habits data for birds are based on crop and gizzard contents of specimens shot for the purpose, while that for game mammals is based largely on evidence left on the vegetation (tooth marks, browsed stubbs, etc.) or direct observations on the mammals while eating.

Particularly in browsing mammals, the identification of the finely masticated paunch contents is always difficult and sometimes impossible. Direct observation of feeding habits from concealment is often better and less laborious. Dixon (1928) has devised a special unit of measurement, which he calls "deer minutes," for comparing the degree to which the various foods at any given time or place are observed to be eaten.

"First, the number of deer that browsed upon each species of plant was noted. The time or duration of each browsing was also recorded. By multiplying the number of deer selecting any species of plant by the minutes spent in browsing, we obtained what we have designated as deer minutes."

Several investigators are now developing a technique for identifying game bird foods in the feces. This will be a valuable alternative where the taking of specimens is difficult or inadvisable.

Depredations on Crops. Game damage to crops is confined principally to deer, rabbits, pheasants, and ducks. Bandtailed pigeons occasionally damage fruit, ruffed grouse sometimes debud fruit trees, and elk damage hay. Other instances of notable damage have occurred, but under combinations of circumstances so rare as to be of only local or temporary importance.

In almost all instances, damage arises from one or more of the following causes:

1. A small area of vulnerable crop thrust into a large area of game range.
2. Drouth, or seasonal scarcity of natural foods or water corresponding to the crop in question.
3. Temporary overabundance of game during the high of the cycle.
4. Temporary concentration of migratory game.
5. Faulty distribution of other game food and cover.
6. Overabundance of game.

Deer damage, such as that described by True (1932) in the foothill orchards of California can clearly be ascribed to 1, 2, and possibly 6, but that described by Crowell (1931) in New England is due to 1 and possibly 6. On the other hand, that described by Frontz (1930) and Clepper (1931) in Pennsylvania is a clear case of overpopulation (6).

The greatest intensity of pheasant damage is usually adjacent to good coverts in country otherwise deficient in cover (5). Several studies of this question are listed in Table 40.

Duck damage, when it occurs, is almost invariably associated with temporary concentrations (4) and ruffed grouse damage with cycle peaks (3). Pigeon damage arises from 1, 2, and 4.

Mechanical means or "scaring devices" for averting damage, such as flashguns, airplanes, and scarecrows have seldom been of lasting benefit (True, 1932*a*, p. 164). Chemical sprays to render the crop repellent sometimes work (True, 1932*a*, p. 160) but are costly, and cannot be applied to ripening fruits. Provision of artificial water has in some cases stopped depredations on fruits. Trained dogs have in some cases kept deer out of orchards.

That even moderate stands of game often do more or less damage should be freely admitted. Experience has frequently shown that the farmer's resentment of this fact is greatly reduced when he is encouraged to derive some revenue from shooting privileges, or otherwise recognized in some degree as the custodian of the state's wild life.

TABLE 40

PUBLICATIONS ON GAME-FOOD HABITS[1]

Compiled in collaboration with W. L. McAtee, U. S. Biological Survey

SPECIES	AUTHOR	DATE	LOCALITY
Almost all game birds	Forbush	1912	Northeast
		1925	General
		1927	General
	Grinnell, Bryant and Storer	1918	California
	Henderson	1927	General
Upland Game Birds	Judd	1905*a* 1905*b*	General
Bobwhite	Judd	1903	General
	Errington	1930	Wisconsin
		1931 *a, b*	Wisconsin
	Harris	1905	Canada
	Stoddard	1931	Southeast
	Bird and Bird	1931	Oklahoma
Cafornia Quail	McAtee and Beal	1912	California
	McLean	1930*a*	California
Gambel Quail	McLean	1930*a*	California
	Gorsuch	1932 (MSS.)	Arizona
Pinnated Grouse	Gross	1930*b*	Wisconsin
Sharptailed Grouse	Lincoln	1923	North Dakota
	Gross	1930*b*	Wisconsin

[1] For full reference see Bibliography.

SPECIES	AUTHOR	DATE	LOCALITY
Ruffed Grouse	McAtee and Beal	1912	General
	Terrill	1924	Canada
	Bartlett	1924	New Hampshire
	Gross	1928*a*	Northeast
		1928*b*	Northeast
	Johnson	1928	New York
	Leffingwell	1931	Washington
	Luttringer	1931*a*	Pennsylvania
Pheasant	McAtee and Beal	1912	General
	Burnett and Maxon	1921	Colorado
	Queen	1927	Idaho
	Cottam	1929	Utah
		1929 (MSS.)	Oregon
	Severin	1930 (MSS.)	South Dakota
	Brown	1931	General
	Leffingwell	1931	Washington
	Swenk	1930	Nebraska
	Rasek	1931	Czecho-Slovakia
Hungarian Partridge	Munro	1925	British Columbia
	Foster	1928	Alberta
	Kelso	1932	Central States and Northwest
	Leffingwell	1931	Washington
Deer	Hall	1927	California
	Bailey	1928	Pennsylvania
	Dixon	1928	California
	Bartlett and Stephenson	1929	Michigan
	Forbes and Bechdel	1931	Pennsylvania
	Clepper	1931	Pennsylvania
	Robinson	1931	Sierra Nevada Mts.
	True	1932	California
		1932*a*	
Ducks:			
Mallard	McAtee	1914	General
		1915	General
		1917	General
		1918	General
	Trautman	1928	Ohio
	Cottam	1930	Florida
Black Duck	McAtee	1915	General
		1917	General
		1918	General
	Trautman	1928	Ohio
Southern Black Duck	McAtee	1914	General
		1915	General
		1917	General
		1918	General
Gadwall	McAtee	1915	General
		1917	General

SPECIES	AUTHOR	DATE	LOCALITY
Gadwall	Mabbott	1920	General
	Cottam	1930	Florida
European Widgeon	McAtee	1917	General
	Mabbott	1920	General
Baldpate	McAtee	1914	General
		1915	General
	Mabbott	1920	General
	Cottam	1930	Florida
Green-winged Teal	McAtee	1914	General
		1915	General
		1917	General
	Mabbott	1920	General
	Cottam	1930	Florida
Blue-winged Teal	McAtee	1914	General
		1915	General
		1917	General
	Mabbott	1920	General
	Cottam	1930	Florida
Cinnamon Teal	McAtee	1915	General
		1917	General
	Mabbott	1920	General
Shoveller	McAtee	1914	General
		1915	General
		1917	General
		1922	General
Pintail	McAtee	1914	General
		1915	General
		1917	General
	Mabbott	1920	General
	Trautman	1928	Ohio
Wood Duck	McAtee	1914	General
		1915	General
		1917	General
	Mabbott	1920	General
	Cottam	1930	Florida
Redhead	McAtee	1915	General
		1917	General
	Cottam	1930	Florida
Canvasback	McAtee	1914	General
		1915	General
		1917	General
	Trautman	1928	Ohio
Scaup Duck	McAtee	1915	General
		1917	General
	Trautman	1928	Ohio
	Cottam	1930	Florida
	Munro and Clemens	1931	British Columbia
Lesser Scaup	McAtee	1914	General
		1915	General
		1917	General
	Trautman	1928	Ohio
	Cottam	1930	Florida

SPECIES	AUTHOR	DATE	LOCALITY
Ring-necked Duck	McAtee	1914	General
		1915	General
		1917	General
	Trautman	1928	Ohio
	Cottam	1930	Florida
Bluebill	Mickle and Thomson	1913	Northern Ontario
Golden-eye	Mickle and Thomson	1913	Northern Ontario
	McAtee	1915	General
		1917	General
	Trautman	1928	Ohio
	Munro and Clemens	1931	British Columbia
Barrow's Golden-eye	Munro and Clemens	1931	British Columbia
Bufflehead	Mickle and Thomson	1913	Northern Ontario
	McAtee	1915	General
		1917	General
	Trautman	1928	Ohio
	Cottam	1930	Florida
	Munro and Clemens	1931	British Columbia
Old Squaw	Munro and Clemens	1931	British Columbia
Pacific Harlequin	Munro and Clemens	1931	British Columbia
Ruddy Duck	McAtee	1914	General
		1915	General
		1917	General
	Trautman	1928	Ohio
	Cottam	1930	Florida
Snow Goose	McAtee	1917	General
Canada Goose	McAtee	1914	General
		1917	General
	Lewis	1931	Eastern Canada
Brant	McAtee	1915	General
	Lewis	1931	Eastern Canada
Shorebirds	McAtee	1911*a*	General
	Wetmore	1925	General
	Pettingill	1932	Woodcock

WATER

Sources of Water. Animals obtain water from four sources, which may be labelled for purposes of game management:

1. *Drinking Water.* This means surface water in the ordinary sense of pools, springs, brooks, etc. As nearly as is known, all game animals utilize drinking water when it is available, whether or no they are dependent on it. Snow is included in this category.
2. *Dew Water.* Many birds drink dewdrops, or water condensed from fogs, when it collects on vegetation.
3. *Succulence.* This means water contained in plant food of

high moisture content, such as fruits, berries, green leaves, sprouts, flowers, and the interior pulp of fleshy plants like cacti. It also includes water contained in animal food of high moisture content, such as insects and insect eggs.

4. *Metabolic Water.* Some species (including many rodents and insects) are now known to possess the ability to convert the carbohydrates eaten as food, or the reserve body fats, into water. Such internally manufactured water is called metabolic water.

No American game species is definitely known to manufacture metabolic water. The non-game species which do so commonly convert and excrete the body wastes as insoluble urates, rather than as soluble uric acid, thus further reducing the physiological water requirement.

Water and Management. The watering habits or preferences of game when water is plentiful, and its real requirements when water is scarce, are two different things. To see a species drinking is not proof that it must drink. To prove that it must drink under one condition of food and weather is not proof that it must drink under any and all conditions. The test of its minimum requirement is the maximum deprivation which it will survive without injury. Game managers, in order to select and develop land for refuges, preserves, plantings, and other management ventures, need two kinds of information about water:

1. The kind and distribution of water-sources *optimum* for productivity under various conditions.
2. The *minimum* kind and distribution of water-sources necessary for survival under various conditions.
3. The environmental controls necessary to meet the second, and if possible the first, criterion.

Reliable information which differentiates the first two points for the various game species under various conditions is scarce and hard to interpret, and not generally available. Most writers confuse 1 and 2. A review of the best available evidence will therefore be attempted. Controls will be discussed later.

Minimum and Optimum Requirements of Game Birds. Stoddard (1928) reports a satisfactory crop of bobwhites in Georgia during the drouth year 1927, in localities where water other than dew and succulence was absent during the nesting season. Many nests a mile from usable drinking water were successfully hatched. During this period water holes were watched from a blind, but no quail came to drink. He concludes that "although no relation between the locations of [356] nests and available surface [drinking] water could be detected, it is significant that the majority were not far from a supply of ripening blackberries." Adults in large pens survived this same drouth on dew, vegetation, limited insects, and an occasional handful of berries. Chicks were reared under the same conditions, with neither water nor milk, but with a regular fruit supply.

Stoddard (1931, p. 500) quotes Starr as finding an abundance of Texan bobwhites "miles from water" during a September drouth when there was no dew. The conclusion reached by Stoddard (p. 501) is that:

> "Bobwhites of all ages regularly drink the dewdrops suspended from grass tips in the morning. If the supply fails, as it sometimes does under certain conditions of wind and atmosphere, berries and green matter are eaten in greater quantity to make up the deficiency."

In short, dew plus succulence is optimum for bobwhite, while succulence alone answers the minimum requirements of the species.

Ligon (unpublished) writes: "Although Mearns and scaled quail drink during the hottest dryest periods when water is available, they can and do live on arid lands without water." He implies that they live without dew, but not that they live without succulence.

Vorhies (1928) asserts that gambel and scaled quail on the Santa Rita Range Reserve in Arizona thrive on succulence alone, seldom have dew, and nest as far as two miles from stock water. They show no concentration of nests near it, nor visible flights to reach it. He confined two Mearns quail for over two months in winter without water, and with no succulence except a few insects and bits of apple. Drinking water offered at the first was ignored.

Gorsuch (1932) finds that apparent concentrations of gambel quail around stock water in Arizona are induced by food (mesquite beans in cattle manure) rather than the water itself. He found nesting pairs as much as four miles from drinking water. Birds seen near water were seldom seen drinking.

Grinnell (1927) writes of California quail:

> "There is, I believe, a critical distance, which, rain or dew failing, is the absolute limit a quail's nest may be located from safely accessible water and result in a matured brood. I estimate . . . that maximum distance to be 400 yards."

McLean (1930*a*) finds the mountain quail of California confined to the vicinity of drinking water, even in winter. He quotes ranchmen, however, as finding the gambel quail as far as 30 miles from drinking water.

The available evidence on the various quails may be summed up in this way: Their minimum requirement seems to be succulence, except in the case of the California quail which seems to require dew (seldom available) or drinking water, and the mountain quail, which seems confined to drinking water. All quail use drinking water when available, but with the exception of the two California species, populations approaching optimum occur on dew and succulence alone.

Surprisingly little is known about the water requirements of grouse. Ligon (unpublished) writes:

> "During the fall and winter, when the prairie hen [of Texas and eastern New Mexico] feeds largely on grain and other dry seeds, they are free to shift about and usually find sufficient [drinking] water to meet their requirements, whereas during the breeding period, when the heat is excessive, and often intensified by prolonged drought, the prairie hen is to be found contentedly located remote from water."

Doze, former state game warden, says of Kansas:

> "Some of our quail live in the sandhills . . . four or five miles from water for long periods of time. It is so dry . . . that there is no dew in the grass, yet the quail *and prairie hen* seem to exist and increase."

Gross and Schmidt tell me they found both the pinnated and sharptail grouse in Wisconsin nesting at least half a mile from drinking water.

S. B. Locke writes me of finding blue grouse nests in Idaho, half a mile from drinking water. It is his opinion that sage hens, sharptail, ruffed and blue grouse in that region nest successfully on dew and succulence alone, but that in late summer after the young become mobile they seek the vicinity of drinking water.

Goldman writes of blue grouse: "I recall that I have seen them in many places far from water."

A. A. Allen writes of ruffed grouse:

> "In captivity, when they have sufficient range and green stuff, they go for days without touching the water in the drinking vessels, or apparently missing it after these go dry. At the same time one frequently sees them drinking. The young grouse in captivity, when given plenty of insects, do not get very thirsty, but without insects or milk curd they do a great deal of drinking."

The *Grouse Report* (p. 92) states that the evidence on the water requirements of red grouse in Britain is conflicting. Young broods survive in captivity without drinking water, but in the wild in late summer the grown birds frequent the vicinity of water, and seem to move away from dry range. Incubating hens commonly seek water when they leave the nest.

The information on grouse is weak in being almost devoid of controlled experimental evidence. It indicates that all American grouse probably nest successfully on dew and succulence, and that the western arid-land pinnated grouse nest on succulence alone. All observers unanimously and independently report a strong tendency for the grown young of most species of grouse to seek the vicinity of drinking water in late summer and fall, but whether they do this out of choice or necessity is not known. Undoubtedly the optimum grouse range should offer frequent drinking water, but the minimum requirement, at least during the breeding season, seems to be dew and succulence alone. In the case of the pinnated (and by analogy the sharptail) succulence, even in the absence of dew, may suffice.

The eastern wild turkey is assumed by all writers to require drinking water, but none of their voluminous testimony seems to differentiate between minimum and optimum conditions. Ligon says of the Merriam turkey of New Mexico: "I know they can survive for extended periods without [drinking] water, but in extremely dry times I think they seek water." We may conclude that the minimum requirement of the western race is succulence, or at most succulence and dew. Possibly the minimum requirement of the eastern turkey is greater, *i. e.*, he may require drinking water. Undoubtedly the optimum turkey range for all races should offer frequent watering places.

The pheasant one must approach with trepidation, considering the widely differing Asiatic habitats of the various species comprising our present hybrids. Allen says: "Ring-necked pheasants require more water than ruffed grouse, but they do not visit drinking places with any such regularity as the mourning dove or valley quail."

Maxwell (1913) says of pheasants: "The provision of water on dry soils is essential to the welfare of the birds." By "dry soils" he evidently means English ranges devoid of natural drinking water. Wight (1930) says of Michigan:

> "Water does not seem to be a factor of importance in the choice of the nest site. During the excessive heat of late July and early August, 1930 . . . pheasant flocks were in some instances found close to water and at times actually in it."

Locke says that

> "In the arid parts of Utah and Idaho nesting of pheasants is confined to well-watered areas, but during the hunting season in southern Idaho the pheasants spread to the sagebrush areas several miles from water."

This evidence as to pheasants is somewhat contradictory. Probably the ringnecks are like grouse: they can nest on dew and succulence, but in late summer tend to seek water either out of choice or necessity. Optimum pheasant range should doubtless offer frequent drinking water.

As to Hungarian partridge, Grange, while at the Wisconsin Game Farm, kept wing-clipped birds all summer in a large pen which was waterless, but for succulence and dew.

Maxwell (1911) is inconclusive. He says of the ideal English partridge manor, "The ground is fortunate in being well watered by a number of springs and streamlets, [so that] a dry summer can be faced with equanimity."

I conclude that Hungarians are like grouse and pheasants:

they can nest on dew and succulence, but in late summer tend to seek water either out of choice or necessity. Optimum partridge range should doubtless offer frequent drinking water.

All observers seem to agree that doves require drinking water daily. One might infer they could exist on dew, but I have no evidence of their doing so. In the arid west, where there is no dew, the evening water-flights of the mourning and white-winged doves are especially conspicuous. In New Mexico they persist in this daily flight even on rainy days when water is available everywhere (Leopold, 1921).

To sum up in terms of minimum requirements: All American upland game birds can nest on succulence and dew except the eastern turkey, the mourning dove, and the California and mountain quails, which seem to require drinking water. In quails, with the exceptions noted, and in pinnated grouse, there is evidence of nesting on succulence alone. Grouse as a group, as well as pheasants and Hungarians, seek and may require drinking water in late summer, and may require it in drouths.

Optimum and Minimum Requirements of Game Mammals. Skinner (1929) says of whitetail deer in the Yellowstone: "They seemed to need water regularly, and presumably drank at least once or twice a day."

Rutledge (1930) says of the eastern states: "Deer will troop out of their regular haunts in very dry weather, if the water supply fails, going to larger streams and rivers."

Burnham says: "Next to moose and caribou as water-loving animals, I should place the whitetail. I think the whitetail requires water every day. Even in the arid country they do not get far from streams."

Newsom (1926) says: "While a deer enjoys playing around water and must have it, he can do quite well with a little."

Lantz (1916) says of whitetail in enclosures: "A good supply of running water must be provided."

Seton (1929) says the nursing whitetail doe waters daily, usually at noon.

Ligon (unpublished) writes me that in the sandhills east ot the Pecos River in New Mexico, and on both sides of the Pecos in west Texas, the local race of whitetails (Odocoileus virginianus texanus) are or were found on range totally devoid of drinking water, and offering succulence alone.

The mule deer evidently differs from the whitetail in its water requirements. Locke writes of the mule deer in the Kaibab:

"For a good part of the summer season deer . . . were quite independent of a direct water supply. . . . The situation changes very definitely as soon as the forage plants become frosted in fall. At that time there is a very definite dependency upon water supply and a concentration in the vicinity of springs or water holes. Observations at the deer traps indicate that at that season deer water . . . every three days."

Hall (1927) says of the mule deer of the Kaibab in summer:

"Does with fawns usually remain within two miles of water. The bucks, barren does, and yearlings . . . may occur far from water. . . . Does bearing fawns concentrate in areas near water, and drink at least once and usually twice each 24 hours. In the first week of July, at which time it rained daily on the Kaibab, does with fawns were found as far as five miles from any lake or spring, but before and after this rainy period none were found further than two miles from . . . water."

McLean (1930*c*) and Hall, in studying the burro deer in Lower California in December, say:

"We saw little if any evidence of places where burro deer had come to water. Most of the 'tanks' . . . showed no evidence of having been used by deer."

Seton (1929) says of the Southwest:

"There can be little doubt that the mule deer or burro deer, like the whitetail, the sheep, and the antelope, dispenses with water altogether . . . where there are neither springs nor pools, but where cactus abounds."

Ligon (unpublished) writes:

"Although desert mountain sheep, antelope, mule deer, peccaries, [and] jackrabbits . . . do drink during the dryest and hottest periods when water is available, they can and do live on arid lands without water."

I conclude that the eastern whitetail deer requires drinking water. Nursing whitetail does seem to require it daily. At least some of the western races of whitetail, however, seem on all fours with the mule deer. In the Northwest, whitetails occur mostly near streams, but in the Southwest they persist on succulence alone.

Mule deer can subsist and fawn on succulence alone. Where water is available, however, does show a strong tendency to seek it during fawning, and all mule deer seek it after frost kills the succulence. Drinking water is doubtless an optimum requirement, but succulence is the minimum.

I have no evidence on the Columbian blacktail. Its range is well watered, like the eastern whitetail's, but the mule deer is a closer relative.

Moose and caribou inhabit well-watered country and seem to drink daily.

Elk seem to parallel mule deer in their requirements. O. J. Murie is conducting experiments to find out.

Skinner (1929) writes me it is his belief that "prong-horns [antelope] in the Yellowstone like water when they can get it easily, and drink daily, but they can go without water for two or three days without discomfort if necessary. They eat snow."

E. R. Sans of the Biological Survey writes me that in Nevada antelope water daily in hot weather, and every two days in cool weather. Nursing does seek the vicinity of water, and drink twice daily. Fawns in captivity drink at all hours of the day.

Ligon's opinion that antelope in New Mexico can and do live on arid land without water has already been quoted.

Burnham writes me that

> "In Wyoming . . . antelope would go to water at a regular time each forenoon . . . but in the Salada Desert of Lower California there are—or were—a good sized band of antelope . . . without any water. The only water is at Tres Posas, where the wells are dug vertically to a depth of 12 or 15 feet, and while we found cougar and coyote tracks, there were no deer or antelope tracks. Dew does not fall. Water does reach this bunch of antelope when the Colorado River [is] in flood in spring."

I conclude that antelope are like mule deer: They drink regularly when they can, especially does at fawning time, but they subsist and reproduce on succulence alone where circumstance requires.

Inquiry about mountain sheep was confined to the desert species, since the others inhabit range well provided with both succulence, water and snow.

Ligon's opinion that sheep in New Mexico can and do live on waterless range has already been quoted. He says: "I have watched mountain sheep avidly eating the thick watery filling of the large prickly pear leaves, which evidently served the purpose of a drink."

Sans watched a spring in Nevada where 80 sheep were watering in October, 1925, and found they came in to drink every three days. He suspects that in July this herd waters every alternate day.

Burnham says of the Salada Desert:

> "We did see evidence that the mountain sheep . . . occasionally come to the tenahas for water. The country, however, is so infested with mountain lions . . . that I think the sheep at times go for days without going to water. At each tenaha we found remains of sheep killed by mountain lions [but] never of antelope or deer, which would have equally fallen a prey to lions, had they been in the habit of watering."

McLean (1930*b*) says of sheep in the Inyo Mountains of California in October: "Lambs do not always come to water with the ewes. . . . The ewes apparently come to water about once every seven days, whereas the rams come every two to four days."

Skinner (unpublished) has seen the same sheep drinking on successive days for weeks at a stretch in the Yellowstone. He believes they there drink regularly at least once a day.

I conclude that the desert races of mountain sheep are much like mule deer and antelope: they drink periodically when they can, but they subsist and reproduce on succulence alone where occasion requires.

Skinner (unpublished) believes Yellowstone bears, both, grizzly and black, ordinarily get enough water with their food He has, however, seen them drinking.

The game rodents may be safely assumed to subsist on succulence alone.

Classification of Requirements. The apparent trend of the foregoing evidence is summed up in Table 41. It should be understood that these classifications are of unequal validity as between species, and that they represent the minimum, not the optimum requirement, under the normal annual range of food and weather. The special effects of extraordinary drouth are covered in the next caption.

The deficiencies in our dependable knowledge of the water requirements of game present a large opportunity for controlled experimentation of the kind performed by Stoddard and Errington for bobwhite. Such experiments have so far been rare, even in species susceptible of confinement, and in species on which a vast amount of unchecked field observation has been expended.

Extreme Drouth. The species listed in Table 41 as subsisting on dew and succulence do not necessarily retain that ability during seasons so dry that there is no dew and little or no succulence. During such extreme drouth the bad effects of water deficiency are also accentuated and obscured by at least two additional sources of direct or indirect mortality:

1. Food shortage.
2. Drying out or undue heating of eggs.

The bad effects of fire and overgrazing are also often suddenly and severely accentuated during extreme drouth.

It is, of course, well known that eggs lose moisture during incubation, and that the loss must not exceed a certain amount, lest the chick become too weak to accomplish his release. It is conceivable that when incubating hens are disturbed during intense heat the sun may "cook" or weaken the eggs, in addition to drying them unduly. The temperature and humidity tolerances of eggs, and the conditions necessary to bring about a normal rate of moisture-loss, are a specific character for each species. This character is known for poultry, but not yet for game species.

Leopold and Ball (1931), in investigating the quail shortage coincident with the drouth of 1930, encountered frequent reports of "addled eggs" in the states whose weather records showed the most abnormal heat and dryness, but none elsewhere. This "addling" may have been induced by hot dry air and soil. While the states which had suffered extreme drouth showed a 30–90 per cent shortage in the quail crop, the adjoining states to the northward showed a decided *increase* in quail in many localities. This seems to confirm Stoddard's conclusion that a moderately

TABLE 41

TENTATIVE SUMMARY OF MINIMUM WATER REQUIREMENTS OF UPLAND AND BIG GAME

Species	Succulence	Dew	Drinking Water	Remarks
Quails				
Bobwhite	X			Juveniles do not need dew
Mearns	X			
Scaled	X			
Gambel	X			
California		X	or X	Need dew or water
Mountain			X	Confined to near water
Grouse				
Pinnated	X	?		Move to water in late summer after young are grown, especially if on dry feed
Sharptail	X	?		
Ruffed	X	and X		
Blue	X	and X		
Sagehen	X	and X		
Pheasant	X	and X		
Hungarian Partridge	X	and X		
Turkey				
Eastern			X	
Merriam	X	and X		
Doves, Mourning & White-wing			X	
Deer				
Eastern Whitetail			X	
Southwestern Whitetail	X			
Mule	X			Nursing does seek water, and all individuals after frost kills succulence, if available
Elk	X			
Antelope	X			
Desert Sheep	X			
Bears	X			
Moose and Caribou			X	
Rabbits, Hares & Squirrels	X			

dry summer is the most favorable, whereas a very hot and dry one may be fatal.

Henry P. Davis found that the quail of the drouth year 1930 near Batesville, Mississippi, weighed 6.17 ounces, whereas on the same ground during the preceding normal year at the same date they had averaged 6.24 ounces in weight. There is every probability that the curtailment of the food supply by the drouth was responsible for this decreased weight, which was doubtless accompanied by a corresponding decrease in vigor.

It has already been pointed out that the southwestern species of quails often fail to pair and nest during years of extreme drouth.

The modified behavior and special cover habits of desert animals in regions of perennial drouth will be described under "Cover" in the next chapter.

In waterfowl, drouth severe enough to dry up the breeding grounds of course suspends productivity altogether. A geographic comparison of recent drouth areas and the breeding ranges of 17 species of ducks, compiled by Hoyes Lloyd, of the Canadian Department of Interior, is reproduced in *Field and Stream* (1929) and also in the Senate Committee Hearings (1932, pp. 204–252).

Control of Water Supply. Probably nowhere is there to be found a more important example of big-scale manipulation of the factors of productivity than the artificial development of watering places for livestock throughout the semi-arid ranges of the West. As in the case of foot-and-mouth disease control in California, this factor was controlled for the benefit of livestock rather than game, yet this very fact emphasizes rather than detracts from its significance. It shows that game management need not always carry the entire cost, or even any of the cost, of control measures. It illustrates the fact that game is not usually a separate product, demanding a separate investment of time or money, with returns proportionate to the separate investment. It is rather a by-product, often demanding only skillful consideration of its needs in conjunction with outlays of time or money that are going to be made in any event, for purposes of agriculture, forestry, animal husbandry, or other economic activities.

Water for livestock has been developed on scores of millions of acres of western ranges. Most of that water is available to and used by game, wherever game has not been eliminated by overgrazing or overhunting.

It is important for the Easterner to realize that water development consists not only of wells and reservoirs which provide water where none previously existed, but includes also the piping and troughing of trampled springs where water existed, but during drouths was lost in rocks or mud. It also includes the opening of easy trails to water previously difficult of access for topographic reasons.

It is important that the relation of watering places to game habitat and movements be thoroughly understood. The relation is best explained by analogy with cattle. Table 41 indicates that most game species are not as dependent on water as cattle are; nevertheless many species not dependent on it regularly use it. The analogy with cattle will help explain the relationship between water, food, weather, predators, etc.

The watering place is the centre of a cow's orbit. Each water has its own separate unit of population. Talbot (1926) has shown that in the Southwest a cow should not have to travel more than about 2½ miles to water in smooth, fairly level country, and not more than 1½ miles in rolling country. A cow's "cruising radius" from water has, under any set of circumstances, a fixed maximum length which depends upon the balance between her input and output of energy.

Forage and water are input. The distance between forage and water tends to increase as the forage near water is cropped down. To reach both with the frequency demanded by her physiological make-up and current condition, a cow must climb hills, endure heat or cold, and escape enemies. These are output. Output must not exceed input if the cow is to live. Hence there is a distance from water beyond which it does not pay to go for food. Shade, salt, disturbance by enemies, and maternal duties influence the balance. Other factors being equal, maximum productivity on a given area is obtained when watering places are so spaced that the "circle" described by the practicable "cruising radius" from each water touches those surrounding the adjoining waters.

An unencumbered, vigorous steer or heifer has a longer cruising radius than a cow with calf, or a heavy bull. All cattle have a longer radius in winter than in summer; in fact, with snow on the ground, water limits become inoperative and other factors such as shelter from storms, and exposure to the warmth of the sun, determine what range is usable. All cattle have a longer radius on a rich range than on an impoverished one. They have a longer radius when the water is clean and abundant, so that they can drink their fill quickly and without interference, than when the water is a mere dribble, or when they are disturbed by predators or campers. They have a longer radius when sufficient salt is properly distributed, than when special foodless and waterless trips to salt grounds are necessary. In short, a cattle country at any one season may be pictured as consisting of water units, each containing food and salt commensurate to its population. The boundaries of the units do not overlap much; they are irregular in shape but tend to be uniform in area, and the area is fixed by the cruising radius of the average individuals in each unit herd.

A game country consists of similar units. As already seen, the *minimum* water requirements of game, and hence the limitations placed on productivity by water supply are usually less than in cattle, but the optimum is not dissimilar, especially in game mammals. We do not know *quantitatively* what they are. This need occasion no surprise when we recall that it is only in recent years that the water requirements of cattle were quantitatively determined, and published as written knowledge. The optimum water requirements or habits of each species of game doubtless vary for every combination of season, food, coverts, and enemies. By discovering these habits or requirements, game management can manipulate them to advantage.

A good illustration is the effect of water spacing on losses from predators. Lions catch mountain sheep by lying in ambush on high rocks which command the trail to water holes. Old-timers say that certain "lookout points" near water holes in the Catalina Mountains of Arizona were formerly littered with the bones of mountain sheep which had been ambushed by mountain lions. If this country had been better watered the lions could not have operated so successfully. A similar instance noted by Burnham on the Salada Desert has already been described.

Since the publication of Grinnell's (1927) findings on the water requirements of juvenile California quail, sportsmen's associations have undertaken "campaigns" to make water from pipelines, and from high-walled inaccessible stock tanks, available for the birds.

Summary. This chapter has necessarily followed down so many ramifications of the subject of food and water control that a summary may help to unify the whole picture, in so far as the scanty evidence permits.

Our understanding of food and water is limited at the outset by our deficient understanding of game physiology.

Game eats a tremendous variety of foods. The bill of fare follows a seasonal sequence, and seems to be determined by availability, palatability, current physiological needs, and previous habit. Exotic foods must be "learned."

During critical seasons, such as winter, the observed sequence probably represents a descending order of palatability or sustenance value, and thus offers valuable clues to food-control measures.

All game birds eat mineral grits, and some species have the ability to conserve their grits when the daily supply is cut off.

Game seldom dies of poisonous foods. It either avoids them instinctively, or learns by experience to avoid them, or is immune, or becomes so with advancing age.

The palatability (and probably composition) of a given food varies by seasons and regions.

Civilization has profoundly changed the kind and distribution of game foods, and has thus destroyed, created, or moved the tenable habitats of species.

Game birds benefit agriculture by eating insects, but it is doubtful whether they control weeds.

The best of various techniques for winter feeding are those which offer several sequences, which are widely interspersed with cover, and which otherwise simulate nature. Spacing should conform to the mobility of the game. Game species differ in aptitude for "helping themselves" to food. Summer succulence sometimes needs to be provided.

Composite analyses of food habits are only a general guide to local questions. Localized food studies are needed.

Water is derived from dew, succulence, and metabolic processes, as well as from springs, brooks, etc. Optimum and minimum water requirements are different. All but two quails can subsist on succulence alone. Most American grouse, partridges, and pheasants require dew as well. The eastern turkey, and all doves require actual drinking water, but the southwestern turkey can subsist on dew and succulence. Big game and rodents can subsist on succulence, except the eastern whitetail, moose, and caribou, which require water. These classifications may break down during extreme drouth, when there is no succulence. Extreme drouth may decrease weights, "addle" eggs, or prevent mating.

The livestock industry has provided game water on large areas of arid range. On such range, the watering place is the centre of the animal's "orbit," and together with food and salt, determines range and population units.

Henry Seidel Canby once said: "The world has become a picture puzzle. When we have put together the few pieces that science has given us, we are often too pleased with our success to be impressed by the result."

We pass now from vine to figtree.

Chapter XII

CONTROL OF COVER

Definitions. "Cover" and "covert" both mean vegetative or other shelter for game.

Strictly speaking, cover is the kind of materials of which the covert is composed. Cover may refer to a single plant or a very small area; covert is a geographic unit of cover.

Plant Successions. Control of vegetation for game cover or food must be based on a thorough understanding of the fact that the kind of vegetation on any piece of land does not remain unchanged from year to year if left to itself. Every acre of soil has a definite sequence of vegetative coverings, and unless accidentally or deliberately interfered with, the type of covering now found will be crowded out by the type next in sequence, and it in turn by the next, until the final or "climax" type is reached. It alone is stable when left alone.

This sequence of changes is called the plant succession. Each combination of soil, climate, and animal life has its own series of vegetative types. A single step in the succession may take a month, or a year, or ten centuries, but its completion is as inexorable as time itself.

The kinds and rates of change vary greatly with soils and climate, and with the kind and degree of interference. In general, the sequence on lands managed for upland game is:

1. Bare ground.
2. Weeds.
3. Grass.
4. Brush.
5. Timber.

Severe interference, such as clearing and cultivation, throws the succession from 5 back to 1. Less severe interference, such as logging, throws 5 back to 4, but if grazing or fire is added, back to 3, or if overgrazing is added, back to 2. The rate of return depends on the continuance of the interference.

Within each of these five classes, there may be a succession of various *kinds* or combinations of weeds, grass, brush, or timber.

This elementary exposition will suffice to show that control of game cover or food is largely a matter of understanding and controlling the plant succession.

So is agriculture, forestry, and range management. Hence the importance of co-ordinating their needs and processes with those of game.

A majority of game species are associated with an interspersion of the early and intermediate stages of plant succession (see Chapter V). Cover control deals with maintaining a *balance* or optimum combination of stages. Stoddard (p. 381) thus sums up this conception of balance for bobwhite:

> "Food and cover are of equal importance to the covey range, and one is of little use without the other. Farms so intensively cultivated and pastured that there is no cover can have no quail; while cover, be it ever so attractive, without suitable food, will be equally barren of birds."

Methods of Cover Control. Cover (and often food) can be controlled by either speeding up or setting back the plant succession. The "tools" used are usually:

FOR SPEEDING UP THE SUCCESSION	FOR SETTING BACK THE SUCCESSION
Planting	Plowing
Protecting against fire	Burning
Fencing against stock	Grazing
	Cutting

These may all be called "natural" tools. It is also possible to build cover artificially by the use of physical objects (brush, wire or lumber), or by changing the quality of the site through fertilization, drainage, or impounding water, and thus changing its plant succession. These may be called artificial tools.

The following captions will set forth the known principles not already explained in Chapter V, and describe practical examples of cover control by some commonly available tools. The game manager may find these suggestive, but he must usually exercise his own ingenuity in devising measures adapted to particular local conditions.

Cover Functions, Quality, and Location. Places to feed, hide, rest, sleep, play, and raise young have been specified as the constituent parts of a habitable range. These generalized categories are really too simple to fit the facts. The game manager working in a particular area needs a very detailed "bill of specifications" as to what constitutes such places, for the species with which he is dealing, *at each season of the year.* He should also know the degree of variation in the composition and interspersion of cover types which his species will tolerate (see Chapter V). For species on which there is no competent monograph, such as Stoddard's on the bobwhite, the manager will have to devise his own specifications. Even if they were all known (which they are not), the presentation of these specifications for all species would far exceed the confines of a single volume. Some samples of cover development on Iowa farms are given in Chapter XV.

It should be emphasized that many special functions of game cover are yet to be discovered. Thus Wight recently discovered that a "crowing area" acceptable to a cock pheasant as a breeding territory probably has more or less definite optimum specifications. His publication (1930) does not give them in detail, but more knowledge will doubtless enable the number of habitable breeding units on any given range to be artificially increased by the manipulation of cover types.

As to quantity or area, game cover is sometimes present in excess of the optimum. This is usually true on cheap, well-watered land, such as the Gulf States and the Lake States. Such quantitative excess, however, is often short of food and lacking in variety, interspersion, or correct density. In parts of Georgia, for instance, Stoddard (p. 370) increased the quail population of large areas of pine undergrown with oak brush by cutting out and thinning the oak, thereby admitting a more vigorous growth of partridge pea, other legumes, weeds, and other foods.

Some deeper explanation is necessary, however, to account for the scarcity of upland game in that vast area of semi-reverted farm land which stretches from New England down the Atlantic seaboard, and which contains more good-looking game cover than almost any other part of the continent. The decline of agriculture has, of course, decreased the food supply, but not everywhere. The lack of interspersion has already been mentioned, but it is not universal. Overkilling has been prevalent, but no worse than elsewhere. Predators may be bad in spots, but no more so than in other regions. I suspect that underneath these locally variable handicaps to productivity runs a more serious and permanent injury: the exhaustion of soil fertility. With the exception of the grouse of the north, which by reason of their bud-eating habit are partially independent of a rich variety of seed-bearing flora, there is a remarkable correlation between game supply and soil fertility throughout North America.

On rich soils and on grazing ranges it is more frequent for game to be limited by a deficiency rather than an excess of coverts. Where agriculture is intensive, full productivity of upland game is usually obtainable only by allowing certain coverts to re-establish themselves through the natural processes of plant succession, or by establishing them artificially through planting. A discussion of artificial covert restoration will bring out the principles involved, and once these are grasped the less difficult problem of allowing coverts to re-establish themselves can be readily solved.

As already pointed out in Chapter V, covert restoration must be founded on a clear realization of function. By discovering the exact kind, amount, and location of coverts requisite for each function, a great economy in acreage and installation cost can be achieved.

Bobwhite quail, for instance, probably reached maximum abundance during that stage of settlement when the composition of their range accidentally reached an equal proportion of brush, woodland, and crude cultivation. It does not follow, however, that the restoration of this proportion is essential in management. A covey of quail may originally have found its requirements for brush satisfied by ten acres of hazel. The reason it was satisfied, however, did not lie in the acreage, but in the accidental existence of a few grapevine tangles, brush piles, or fallen treetops occurring in the hazel, but aggregating only half an acre in total area. In short, the function of the ten acres of hazel brush was concentrated on a twentieth of its total area. By restoring either the particular things formerly discharging this function, or their equivalent in plants or structures having the same properties, a satisfactory quail population might be restored by management without the "expenditure" of more than a fraction of the acreage formerly used. In short, restoration is a matter of simulating the quality, rather than the quantity, of original coverts. That acreage will suffice which represents the minimum necessary to balance the food supply, that is, the minimum admissible under the environmental tolerance of the species.

Quality is a matter of location as well as properties. Thus a grapevine tangle for quail on a sunny bank with a south exposure and protection from wind, and with usable avenues of travel in the form of brushy fencerows leading out into the food types, might readily add a new covey to the game population of the farm, when the same tangle situated in the middle of a bare field, or on the north edge of the woodlot, might have no effect at all.

Kinds of Cover. For convenience in the ensuing discussions, five common functions of cover may be given special names:

1. Winter cover. Vegetation offering invisibility or mechanical protection during snow.
2. Refuge cover. Vegetation from which game cannot be driven by hunters.
3. Loafing cover. A place, not necessarily large, often near 1 or 2, and offering shade in summer or sun and wind-protection in winter.
4. Nesting cover.
5. Roosting cover.

There is, of course, some overlap. The term "escape cover" often applies to 1 and 2 collectively.

Some of these categories cannot be satisfactorily discussed, because the requirements of the different species are so variable that a discussion would fill a volume. Errington (1931*c*) describes winter cover for bobwhite, and Stoddard gives a complete inventory of the needs of this species. The *Game Survey* (p. 59) gives a general appraisal of cover conditions and trends.

All farm game, however, has similar nesting requirements. A discussion of nesting cover follows.

Theory of Nesting Cover. "Bait" Cover. It is only in the last few years that game managers in this country have recognized nesting cover as a separate and distinct need. We now realize that a range with ample winter cover may be radically deficient in nesting cover, or vice versa. The American inception of the idea goes back to Stoddard (1931). It has been amplified by several recent investigators, especially Wight (1930) and Yeatter (1932).

Methods of diagnosis for nesting problems in general are expanded in Chapter XV. We are here dealing only with cover.

Most of the breeding ranges of our ground-nesting birds offer an infinite amount and variety of nesting cover after the new green growth of the year has started. Most of our waterfowl and all of our gallinaceous birds, however, tend to *start* nesting *before* the new green growth has become serviceable. Their ultimate success in raising a brood depends on the outcome of a series of repeated nesting attempts following successive previous failures. When one of these attempts at last succeeds the breeding is over for the year.

The longer the period available for "repeat nests" the greater the probability of ultimate success. We do not know what terminates the period if none of the successive attempts succeed. It may be weather or it may be physical exhaustion. It seems certain, though, that the laws of chance will raise the probability of success if we lengthen the period at its anterior end by providing nesting cover of the *previous year's growth*, which stands ready as soon as the birds are ready. Such cover may induce earlier nesting and it certainly lowers mortality from nest destroyers.

Moreover late nests in agricultural crops are endangered by harvesting machinery. The more nests we can decoy into other cover the less will be the loss of nests in crops. "Bait cover" is cover deliberately provided to keep nests out of crops or other dangerous ground.

There is reason to suspect that in the absence of special nesting cover, the plant and crop succession on certain ranges for certain species is such as to hold ready a new and accurately timed misfortune for every successive nesting attempt. Thus a bird forced to build her first nest in early May in the old grass of a narrow fencerow is robbed by a crow using the fenceposts as ready-made observation towers. Her second attempt is made in alfalfa which has become serviceable just at that time, only to expose the nest when the alfalfa is cut in June. Her third attempt is made in oats, then still uncut, only to fall victim to the harvest in July. Under such conditions nesting cover is clearly a limiting factor, and successful management must begin by either providing bait-cover or adopting mechanical means of saving the nests in hay and grain.

Control of Nesting Cover. Marginal strips of hay or grain left standing from the previous year are often effective "bait." Thus Wight (1930) finds that hayfields are a favorite location for late pheasant nests in southern Michigan, and that nearly all of the nests are located in the outer four or five "swaths" of the hay cutter. The hen uses the fencerow as a "street," and enters the hay only far enough to hide the nest. Assuming that some hay could be left uncut as "bait" for pheasants, it would be just as effective and much more economical to leave only the periphery of the field. The function of the hayfield as a nesting covert is all concentrated in its edges. Leaving the outer two or three swaths uncut on one or two sides of a hayfield during the last haymowing in fall would "catch" most of the early nests next spring. At the second cutting, after the nests have hatched off, this marginal strip could be taken as usual, but a new strip left for the succeeding year's nests on some other side of the field. A rotation of bait coverts is thus established without undue sacrifice of acreage. Incidentally the bait strips would have some value for winter cover as well, especially when snow is absent. The same principle of rotation of margins can be used in grainfields by letting stalks and weeds stand.

Yeatter (1932) likewise finds that over half of the Hungarian nests found in the fields of southeastern Michigan and northwestern Ohio lie within 30 feet of the edge, and over half of all nests found were in hay or grain, especially alfalfa. The most frequent hatching date falls between June 15 and June 30. The first alfalfa cutting begins June 10, so that most alfalfa nests are destroyed by the mowing. Farm machinery of one sort or another accounted for 40 per cent of all nest losses and about 25 per cent of all nests found.

The losses in cutting small grain are less than in mowing hay because the early nests hatch before the grain is cut. "It seems likely that the majority of the nests destroyed in [the grain] harvest are those of birds whose nests have previously been broken up during haying."

Yeatter tried out, and found feasible, the following technique for detecting hayfield nests before mowing: Drag the outer edge of each hayfield with a rope pulled by two men walking abreast.

Do this at a date when the nesting studies show the average incubation is well enough advanced to avoid risk of desertion. Find and stake the nests indicated by the rope-flushed hens, and then in the subsequent mowing leave a small "island" of uncut hay around each stake. Observations indicate that hens will return and hatch nests in such "islands" of cover, whereas they usually desert nests cut over by the mower.

To avoid the labor involved in Yeatter's rope-dragging technique, Conservation Warden Arthur Peterson (1931) has devised a "flushing rod," extending from the outer end of the cutter to the harness on the shoulder of the near horse, in such a manner as to brush the tops of the hay, and thus automatically flush any birds in time to allow the driver to stop the team and investigate. If there is a nest, an island of uncut hay can be left. The Peterson flushing rod is shown in Fig. 27.

The idea of mechanical flushers has been adapted to many varying conditions. Iowa (*Handbook*, p. 34) uses a flapping canvas, hung from a rod tied to the neckyokes; Minnesota a rod bolted to the doubletrees; Pennsylvania a rod hung with sleighbells.

To provide nesting and loafing ground for quail, Stoddard (p. 364) left unplowed strips on the edges of fields adjoining escape coverts. His main control of nesting cover, however, was the thinning of reverted broom sedge fields by controlled fire, so as to get the medium density of grass desired for nesting purposes.

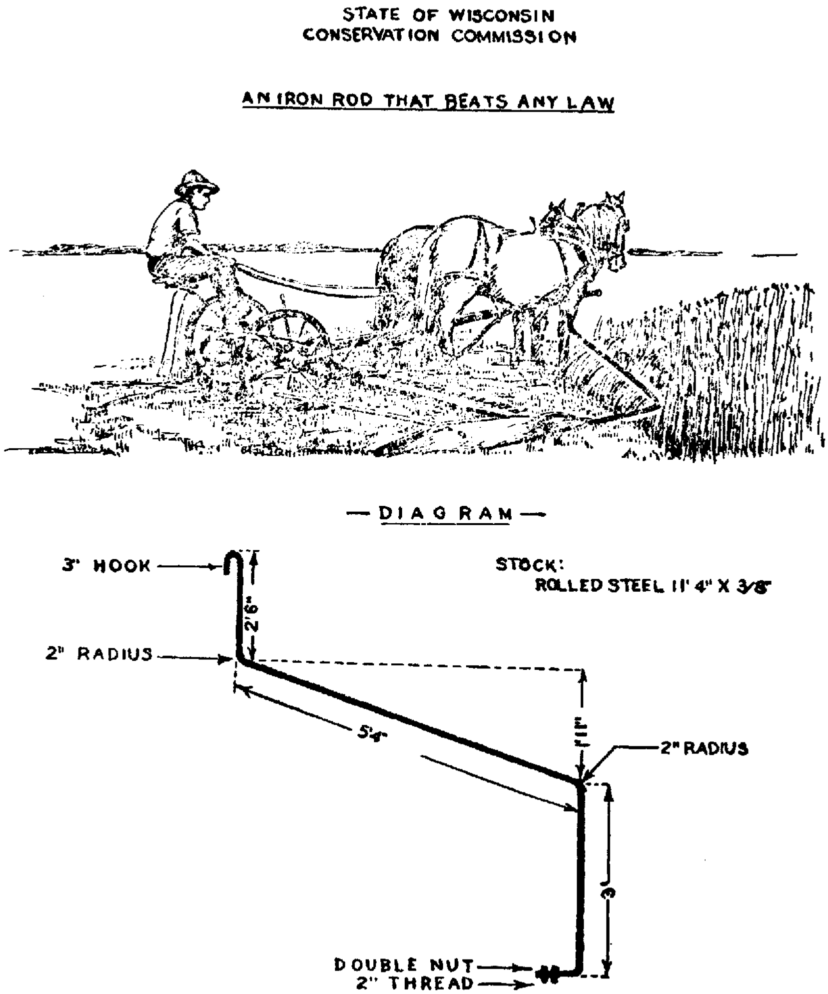
In cutting fields containing partridge chicks, Maxwell (1911) advises working the mower from the edges toward the centre, and then leaving a centre-strip uncut overnight, so as to give the entrapped broods time to disperse to other fields.

Nesting cover for red grouse in Britain consists of low (young) heather. Long old heather is never used as a nesting site. Heather about a foot high, at the edge of an opening, is preferred. Nest-cover control in red grouse is therefore a matter of bringing about a high degree of interspersion of age-classes of heather. This is accomplished by spot-burning under careful control (Leopold and Ball, 1931*a*).

Nesting coverts on dangerous ground may act as a trap, and do more harm than good. Stoddard (p. 369) deliberately burned the nesting cover on land known to overflow yearly, thus forcing the nesting bobwhites to seek the safer uplands.

FIG. 27

PETERSON FLUSHING ROD



In the arid west, nesting cover for waterfowl on the shores of lakes and reservoirs is often removed through grazing, and nests destroyed by the trampling of livestock. Fencing such shore-lines in a series of enclosures, with the necessary open "water gaps" between them to allow the stock ample access to water, would vastly enhance their productivity by providing cover and protection for nests. Fencing only the marshy portions, and leaving gaps at the hard portions of the shore would also tend to prevent the "bogging" of weak cattle in spring, and thus improve conditions for livestock as well as ducks.

It is safe to assert as a general principle that the leaving of dry grass of the preceding year's growth, not too rank or dense, in strategic spots, will "capture" most of the early nests of game birds, and possibly even induce earlier nesting. By then protecting this "bait" cover against enemies (including plow, fire, grazing, and predators) three purposes are accomplished: (1) nest mortality from agricultural machinery and livestock is reduced, (2) survival chances are increased, (3) earlier and larger young are produced. In America we do not yet discriminate against renestings and their resultant late young—a bird is a bird, and that's that. We even refrain from shooting "squealers" on ethical grounds. But in Britain late young are regarded as a "menace to the health of the moor" because they emerge from the winter "weak, and a fit host to disease." A deliberate attempt is made to kill them off during the fall shooting (Leopold and Ball, 1931*a*). The English idea seems the sounder. The only contrary argument is the possibility that early broods run stronger to males than late ones (see Chapter IV).

Concrete examples of nesting cover controls, in combination with other range developments, are shown for Iowa pheasants in Fig. 22 and for Iowa quail in Fig. 33.

A set of directions for nesting cover control, written in layman's language, is given in the Handbook *Management of Upland Game Birds in Iowa.*

Properties of Winter Cover Plants. Economy in acreage and installation costs calls for the utmost care in the selection of cover species, either for artificial planting or for natural reproduction. Such economy is obtained only by combining as many properties as possible in a single species of plant.

In snow country, the most essential property is dense winter foliage or thorns. Dense winter foliage is obtainable only in nondeciduous or evergreen species, such as the conifers. Dense foliage is not necessary if the cover has thorns (osage, rose), or if the branches are so matted as to exclude predators without either thorns or foliage (grape tangles). Whatever the property, an effective cover for either escape or shelter must be close to the ground. Thus evergreens are effective only as saplings raised in the open, because then only do their lower branches persist and sweep the ground. Osage is best when the lower branches are pendant, and grape when the tangle of vines is on or near ground levels. Old evergreens with clean boles are useful to many small birds, but useless to game except as emergency tree-roosts during blizzards. Most upland game bird species have been known to resort to such roosts in bad weather.

The next most important characteristic is low installation cost. This gives a great advantage to the species which can be propagated by cuttings (osage, willow, grape) or by planting root-suckers or root-cuttings (plum, some roses). Transportation costs are also reduced if wild stock, as distinguished from stock purchased from a nursery, is available. The availability of wild stock, of course, varies as between species and localities.

The next most important property is vigor. This includes ability to reproduce by sprouts if cut or burned, ability to spread by means of root-sprouts, and ability to make quick growth. Most species other than conifers have the property of quick growth, especially willows.

Next comes resistance to grazing, drouth, shade, and fire. On heavily pastured land grazing resistance is essential, unless the plantation be surrounded by a small gateless fence. Spruce, cedar, and osage are examples of cover plants not eaten by stock. Rabbit browsing sometimes injures plantings, and cannot, of course, be avoided by fencing, except at heavy cost for small-mesh wire.

Drouth resistance is important mainly in arid districts where coverts can be most economically placed on non-irrigated land. Russian olive and tamarisk are outstanding for survival without irrigation. They will not, however, thrive without some degree of subterranean moisture.

Tolerance of shade is necessary wherever a covert is to be placed in woodland. Even the tolerant species require some opening of the forest canopy to insure vigorous growth.

Although many of the species listed in Table 42 have the other properties of resistance, none of them resist fire, except in the sense of resprouting if they are burned.

A very important item of resistance is ability to make a start in spite of competition by grass and weeds. Few species can be successfully planted in heavy grass without plowing a furrow, or removing the sod from the planting spot, or smothering it by a heavy mulch.

It is desirable that cover plants produce food as well as shelter. Wild grapevines, plums, and haws are outstanding in this respect.

It is desirable that game cover plants also have value for song and insectivorous birds. Most of the hedge-forming species, as well as conifers and grapevines, are much used by bush-nesting species and by winter visitants.

In case plantings are installed on boundaries of fields, it is sometimes desirable to select a species which can be pruned as a hedge, thus dispensing with a fence. Osage is outstanding in this respect.

In case cover is to be installed on land subject to erosion, it is important to select a species with dense fibrous roots. Willow and osage, for instance, represent the extremes of matted and attentuated root systems respectively.

Lastly cover plants should be unobjectionable from the agricultural standpoint. In many regions the osage, for instance, is host for the San Jose scale, and can therefore not be tolerated in the neighborhood of commercial orchards. Likewise red cedar is host for certain rusts, and hence is undesirable in the neighborhood of apple orchards. For this same reason, cedar and crab-apple should never be planted together.

Table 42 summarizes the properties of typical cover-plant species.

In many instances it is desirable to combine two or more species in the same covert, in order to get a larger range of properties, and in order to offset the defects of one by the merits of the other. Thus Norway spruce appears to have all the properties desirable for a winter escape-covert for quail, but compared with the other species its growth is slow. If, therefore, a clump of Norway spruce be surrounded by quick-growing thorny roses, the immediate value of the plantation is probably enhanced, and its ultimate value improved. The coniferous clumps shown in the accompanying photograph installed by the University of Wisconsin have been surrounded by plantings of prairie rose (*R. segetaria*) and sweetbriar (*R. rubiginosa*) to test out this idea, and to compare the value of two species of rose for this purpose.

TABLE 42

PROPERTIES OF TYPICAL PLANTS SUITABLE FOR ESCAPE-COVERTS FOR UPLAND GAME

Legend: ▨ Notable value
O Notable deficiency

Species of Plant	Winter Value		Cost and Availability				Vigor			Resistance			Bird Value	Fence Value	Food Value		Pest Risk			Special Properties
	Evergreen foliage	Thorns (or equivalent)	Propagates by cuttings	Wild stock available	Stocked by nurseries		Coppices if cut or burned	Spreads by root-sprouts	Quick growth	To Grazing	To Drouth	To Shade	Harborage for insectivorous birds	Can be pruned as a hedge	Valuable winter fruit	Valuable summer fruit	Harbors insect pests	Harbors diseases	Kind of pest	
Norway Spruce	▨	▨			▨					▨		▨	▨							e i
White Pine	▨				▨															b e
White Cedar	▨				▨				O			▨	▨	▨						b e
Red Cedar	▨			▨	▨				O	▨	▨		▨	▨	▨			O	Apple Rust	c e h
Osage Orange		▨	▨	▨	▨		▨		▨	▨		O	▨	▨			O		San Jose Scale	a c f
Tamarisk			▨	▨	▨		▨		▨	▨	▨			▨						a c g i
Russian Olive		▨	▨		▨		▨		▨	▨	▨				▨					c e g i
Wild Plum		▨		▨	▨		▨	▨	▨	▨			▨	▨		▨				e d
Red Haw		▨		▨	▨		▨			▨			▨	▨	▨					d e h
Crabapple		▨		▨	▨		▨						▨							e h
Wild Grape		▨		▨	▨		▨		▨				▨		▨	▨				b e
Blackberry		▨		▨	▨		▨	▨	▨	▨		▨				▨				b f
Raspberry		▨		▨	▨		▨	▨	▨			▨				▨				b f
Bush Willow			▨	▨	▨		▨	▨	▨											b g
Rose (setigera or rubiginosa)		▨		▨	▨		▨	▨	▨						▨					e f
Buckthorn (Rhamnus cathartica)		▨	▨		▨					▨		▨	▨	▨	▨	▨		O	Oat Rust	f i

a. Not frosthardy in Lake States.
b. Injured by heavy grazing. Should be fenced.
c. Never browsed by stock.
d. Improved by grazing because of hedge habit.
e. Valuable to game mainly when branches hang near ground.
f. Suitable to plant around conifer groups to add thorns and afford cover while conifer are growing.
g. Suitable for ditchbanks and waste corners in arid climates.
h. Do not plant apples and cedars together.
i. Exotic species.

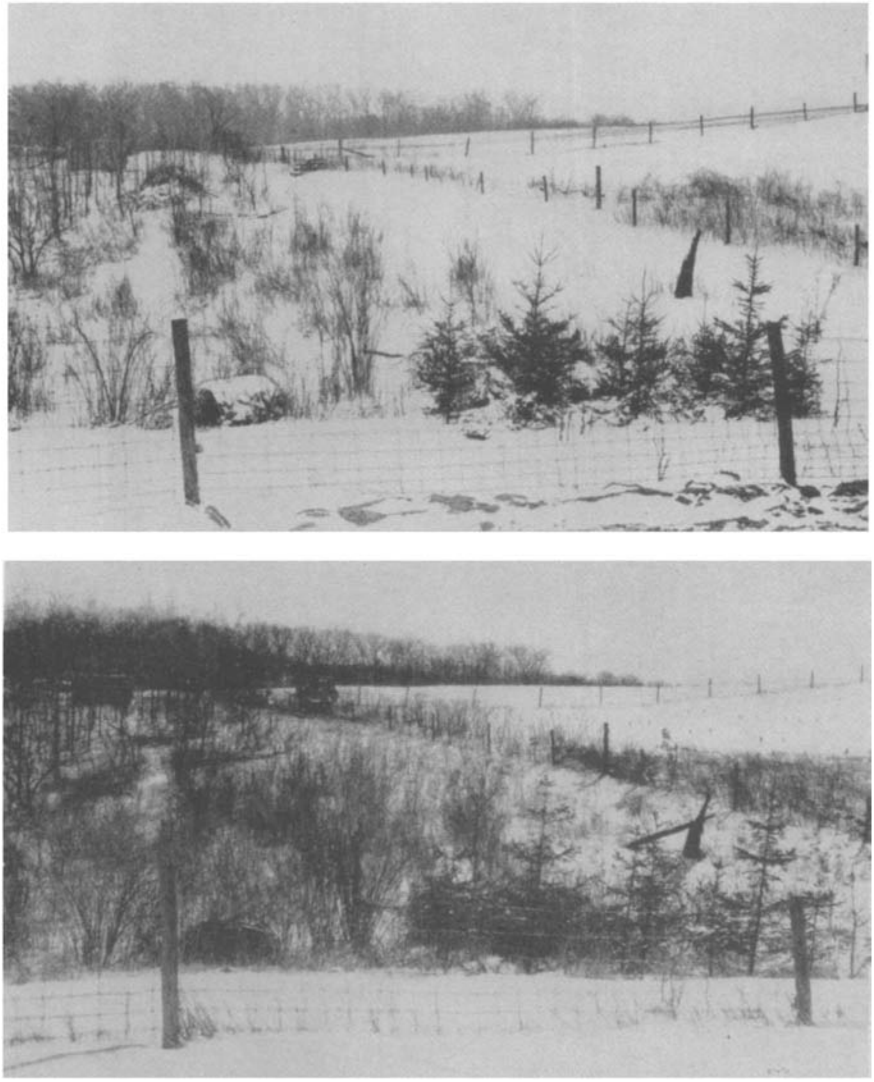


FIG. 28. One year's protection against grazing restored this covert to a habitable condition for quail. The Norway spruces in the foreground were planted by the University of Wisconsin to test the value of conifers as escape-cover.

FIG. 29. Norway spruce under black locust grows faster than away from locust. In the upper picture, under locust, the trees are thrice a man's height; in the lower one, only twice. The locust, like alfalfa, fixes nitrogen from the air. (Photo by Michigan School of Forestry and Conservation.)

There is large opportunity in cover control for the skillful application of specialized knowledge of forestry and soils. For example: in the demonstration forest operated by the Michigan Forest School it has been found that Norway spruce planted under black locust, or on land which has recently carried this tree, grows much more rapidly and vigorously than on adjacent land without locust. Fig. 29 shows the difference, (*a*) being three times the height of a man, and (*b*) only two times. The reason is that locust is a legume and fertilizes the soil by nitrogen fixation, just as alfalfa or clover does. Locust thickets frequently occupy waste corners suitable for game coverts.

It is often not necessary to charge the entire cost of a plantation against game. Thus a clump of spruces situated in a waste corner of a farm may have a landscape value quite sufficient to justify the cost.

Escape coverts, unless naturally present, are necessary to the full success of winter feeding stations. A successful winter feeding station is located in the thicket just to the left of the centre of the photograph in Fig. 28. This photograph also illustrates what is usually the cheapest way to restore cover: the exclusion of grazing. The upper view, taken in 1929 after cattle had been admitted to this covert all summer, shows that the density had been reduced below that necessary to hold quail during snowy periods. The lower view, taken in 1930, shows what one year's protection against grazing can accomplish. The density is now sufficient to winter a covey.

Quick and Substitute Coverts. On bare areas even the quickest-growing cover plants require several years after planting to become effective in holding game. A more immediate effect can sometimes be obtained by semi-mechanical expedients, of which several examples applicable to farm game will be given.

One of the quickest ways to reinforce a deficient winter covert is to fell branchy trees with the leaves on, and leave the tops unlopped. Oak leaves are particularly persistent on summer-cut tops. If in pasture, the fallen top should be fenced so that grass, weeds, and vines can come up through it. Seeding a few spots on its outer edge with false climbing buckwheat, or planting a few wild-grape cuttings, will add density, permanence, and food. I have seen a leafy tree-top, accidentally left by the farmer, hold a covey of quail where in previous years the natural cover was not quite enough to do so. Ruffed grouse and cottontails are also fond of leafy tops.

A modification of the tree-top idea is to select a tree already bearing a grapevine, and cut the tree *but not the grape*. Enough surrounding trees must be cut to give the grape light. Such a vine, being strongly rooted, will cover the down top with a mat of vines in a single season.

A clump of discarded Christmas trees makes a good covert for the rest of the winter.

Errington (1931*c*) finds that shelter roofs built of lumber are apparently not attractive to quail, even when open on three sides and camouflaged with brush. Quail enter them only if food is placed beneath, or only to the extent that they would enter the brush without the roof.

Brush stacked against a log or pole is good but temporary.

Loose rolls of discarded woven wire are freely used by quail and cottontails, especially if camouflaged with brush and covered with vines. There is an astonishing quantity of such old wire available in the "dumps" of some farming regions.

The very best of all bedding grounds for cottontails results when stiff crooked brush, such as oak loppings, is placed in small piles upon a strong bluegrass sod. During the succeeding summer the grass, being mechanically sustained and protected from grazing by the brushpile, grows up through it and weaves a warm dry airy structure ideal for "beds." Rabbit-heaven consists of a south sloping pasture studded with such grassy brushpiles, with an uncut cornfield below, and a briar-patch on the top of the hill.

None of these artificial expedients will hold game unless correctly located, nor unless adjacent to almost-sufficient natural coverts and to adequate food. The best location is a south-facing bank offering sun-exposure and wind-protection. They merely serve to bolster up a range which has become a little too bare to be reliable. Usually there should be a number of substitute coverts of the same sort, so that the game will not have to "bush-up" daily in exactly the same spot, and thus become too well known to its enemies.

"*Streets*." Coverts must have convenient routes of ingress and egress. These routes or "streets" should connect the covert with the feeding ground, and, if possible, with other coverts. A street for us is a route clear enough to be travelled with ease; a street for game is a route with obstructions enough to be travelled with safety.

Brushy fencerows, gullies, or other strips of vegetation are the usual routes. Even a row of cornshocks may be used as a route of daily travel. When there is no safe route of travel, most game birds fly to the feeding ground, but any range is more attractive if its component parts can be reached without the necessity of flight.

On the ordinary farm the places to be connected with travel routes are the feeding ground (weed patches, shocked or standing corn), the woodlot, and the barnyard or feedlot.

On the Georgia quail preserves Stoddard (p. 371), by leaving unplowed strips, deliberately subdivided large fields with "streets" of weeds or briers. Wild plums were sometimes planted artificially in these strips. On terraced land, streets are often automatically provided if the embankments are left unplowed. The widespread menace of soil erosion (Bennett and Chapline, 1928, *Game Survey*, p. 247) prompts the hope that increasing areas of farm land will be terraced, and thus improved as farms, watersheds, and game ranges.

Streets form an important part of the cover improvements for pheasants installed by Wight (1931) on the Williamston Project in Michigan. The isolated glacial potholes offer excellent winter and refuge cover, but are often far apart. The stand of pheasants is being built up mainly by installing "streets" and food patches.

Streets left for game serve as nesting sites as well as travel routes, especially for bobwhite and Hungarian partridge.

Shade. It seems probable that the minimum water requirement of some animals varies not only with the available food but with the available "cover" furnishing shade and humidity. I am permitted to quote the following unpublished observations of J. S. Ligon on the game of arid New Mexico:

"During the hot, dry summer days animals and birds alike retire to the shelter of caves, over-hanging ledges, canyons, or dense cover of various shrubs, where in complete retirement and dense shade the consuming rays of the sun are avoided.

"In the range of the desert dwelling mountain sheep almost invariably are to be found caves of considerable extent in which the sheep spend the days, not venturing forth until tempted by the long inviting shadows of late afternoon. In such retreats, by pawing, clawing, or scratching the various species come in contact with the cool, soothing earth. In sheep caves, damp spots and sometimes even traces of seeps are encountered and used by the sheep.

"Jack rabbits furnish a good example of the persistence of desert inhabitants in clinging to shelter against the rays of the sun. Though remaining in comparatively open spaces where escape from enemies is possible, they scratch out their forms in accordance with the morning shadow cast by some sheltering shrub, and shift their position with the change of the shade, winding up the day on the east side of their retreat. Cottontails are even more earthly, generally remaining in burrows during the day.

"Peccaries, like the desert dwelling sheep, are fond of idling away the day in caves or, in the absence of these, under dense growth of spreading mountain shrubs.

"Ample cover to insure protection against the direct rays of the sun is also a range requirement of scale, gambel, and Mearns quail."

It has long been known that the desert forms of mountain sheep resort to caves, where their remains are frequently found, but it has usually been supposed that they sought caves for shelter from winter storms, rather than from summer heat. Ligon's observations now indicate that caves are a "special factor" for sheep, and probably control their distribution in the waterless portions of their range, where scant succulence is their sole source of water supply during dry periods.

Inter-relation of Cover and Food. Just as the desert sheep seems to depend for its existence on a specialized kind of cover, so Schierbeck (1911) claims the deer of Nova Scotia depend for their welfare on the combination of hemlock forest and yew browse. The yew shrub or "ground hemlock" (*Taxus canadensis*), he says is the winter food of deer, and grows only under hemlock forest (*Tsuga canadensis*).

"The cutting of the hemlock stands causes the ground hemlock to disappear, as it can only exist in the shade of the hemlock trees. I have noted the disappearance or diminution of the deer stand where old hemlock stands have been cut."

Schierbeck traces a similar intimate relationship between caribou, reindeer moss, and fire in Nova Scotia. Moss is the winter food of caribou. It comes back in 30–40 years as the first stage of the plant succession after fire. Forest is the second stage. There were heavy fires during the eighties. "Those fires destroyed the reindeer-moss and today, as a consequence, the caribou have disappeared. The reindeer-moss is now coming back, but I doubt if the caribou will follow it."

A relationship not far from dependence is observed by Gorsuch (1932) to exist between gambel quail and desert hackberry (*Celtis pallida*) in Arizona. This evergreen hackberry is a dense thorny shrub furnishing both shade, escape cover, roosting and loafing cover, and food. I have long observed a similar dependence of scaled quail in central New Mexico on the chamisa bush (*Atriplex canescens*). Hackberry and chamisa might well be called "index" plants for quail, because where these plants are scarce the presence of a single specimen is as sure an indicator of the whereabouts of a covey as the direction of the nose on a pointing bird dog. This rule is especially infallible at midday, when the birds spend their loafing hours under the airy shade of their evergreen umbrellas.

Red grouse derive most of their food and cover from the various ages of heather, but they have been known to exist on heatherless range. Nevertheless the greater part of grouse management is heather control, and heather is in one sense an index-plant for the species.

These various examples point out their own lesson to the game manager: watch for "key" plants, and if there is an undersupply or faulty distribution, correct it by reversing the action of the same "tools" which brought about the scarcity. Thus chamisa is eliminated by overgrazing. Lighten or exclude the grazing and it comes back.

Other Crops and Game Cover. Sweeping statements are often made as to the detrimental effects of fire, grazing, and drainage, or beneficial effects of forestry on game range. Such statements cannot possibly be true. It is self-evident that the effect varies with the kind of game, the composition and interspersion of the food and cover, and the intensity, frequency, size and season of these "influences." The game manager should beware of rules of thumb.

Stoddard's chapter on "The Use and Abuse of Fire" is as good an exposition as I know on the principles and practices of fire control as related to game.

The *Game Survey* deals throughout with the effects of grazing, farming, and lumbering on game cover and food.

Leopold (1930*a*) deals with a few favorable and unfavorable effects of various silvicultural and grazing systems on game environment, and (1931*b*) with the rôle of forestry in game management.

Grange, in a forthcoming farmers' bulletin, will deal with the modification of farming methods for game-management purposes.

No writer has as yet adequately dealt with the effects of game cover on the conservation of watersheds.

Fire as a direct source of mortality in game, will be dealt with in the chapter on "Accidents."

Summary. Cover is controlled by controlling the plant succession in the right direction at the right time and place. Cow, plow, axe, and fire reverse the succession. Fencing, fire-protection, and planting advance it.

Cover functions include shelter, escape, refuge, loafing, nesting, roosting, shade, and sun. Function is often localized in a small component of a given acreage or type, and for any given species varies with season and with the incidence of food, predators, and other factors. Location, shape, and area must be related to function.

Nesting cover of the previous year's growth is needed to encourage early nests and keep nests out of crops where they are destroyed by machinery. Nests are usually on the margins of any solid block of cover, such as a hayfield. Mechanical flushing devices can be used to locate such nests.

Cover plants should be selected for their properties such as foliage, cost, vigor, resistance, food and fence value, and pest risk. Temporary substitute coverts can be built of brush or quick-growing plants.

Some plant species are so necessary to certain game animals as to control their distribution and daily movements. They may be called index plants.

Industrial uses of land profoundly alter game cover, for better or for worse. If controlled, they become valuable tools for game management.

Elbert Hubbard made one epigram which is not only pithy, but also profound. He said: "To plow is to pray."

One of the defects of our mechanized society is the decreasing proportion of people privileged to plow.

The manipulation of game ranges is a new form of "plowing."

Chapter XIII

CONTROL OF DISEASE

This chapter is not a compendium of available knowledge on game diseases. Larger volumes than this have been written about a single disease of a single species.

It aims rather to sketch, in bold outlines, the probable rôle of the disease factor in game productivity, and the possibilities of its control in game management. The principal purpose is to help the game manager or thinking sportsman orient his mental picture of the mechanisms, scope, and power of wild-animal diseases in the light of what is now known about them, so that his field observations can be pertinent and his co-operation with specialists more intelligent.

New knowledge is piling up rapidly. If the reader has biological training, he may have to unlearn certain principles which were taught him a few years ago as accepted truth. By the same token, this sketch may not long remain up-to-date.

It is a pity that the narratives of scientific exploration in this field—as fantastic a romance as any Arabian Nights—should either be masked by such technical verbiage as to mean nothing to the thinking layman, or translated for the popular press in such kindergarten terms as to be no longer true. These explorations have divulged a fabric of relationships in the biotic community of great import not alone to conservation, but to sociology and philosophy as well.

Take, for instance, the growing realization that disease organisms, despite their ruthless decimation of individuals, tend constantly to evolve toward a symbiotic relationship—*i. e.*, a relation of mutual tolerance—to their host species. We have already seen a hint of something parallel in predators, and the tendency of the game itself to remain in or return to some sort of equilibrium with the capacity of its environment seems to be merely another expression of the same thing.

It is not for this book to suggest social interpretations of these phenomena, but the game manager, if he is so disposed, may well regard his field as an outdoor laboratory for the study of *Homo sapiens*.

Importance of Disease. The rôle of disease in wild-life conservation has probably been radically underestimated.

Disease, for instance, is not commonly thought of as controlling predators as well as game, yet the drift of the recent evidence is strongly in this direction, especially mammalian predators.

That disease is the outstanding control of buffer foods for predators, such as rodents, is now in many instances an established fact.

There are grounds for suspecting that disease may in some cases be the factor which delimits the geographic range of game species.

Density limits of game populations are in many species probably set by disease. This has long been asserted as a generalization, but recent years have begun to show specific cases.

Density fluctuations, such as cycles and irruptions, are almost certainly fluctuations in the prevalence of, virulence of, or resistance to diseases. Some diseases also disturb the sex ratio, and may affect fertility.

This long-prevailing under-valuation of the disease factor may be definitely associated with the limitations of the observational method in studying natural history. It is difficult or impossible to "observe" disease, because of the promptness with which diseased wild animals disappear or succumb to natural enemies. In most species it is only during epizootics, when the sick or dead become so numerous as to satiate all the predators, that they are seen at all. Hence disease did not yield to the observational method of study. Understanding began only when field observations were combined with the experimental or laboratory technique of modern science.

Feasibility of Control. Most laymen and many scientists entertain mental reservations as to the practical utility of wild-animal disease studies. "You cannot doctor sick birds." With this terse and (to his mind) conclusive rejoinder the layman often attempts to relegate the whole subject to the category of interesting but useless knowledge.

He, of course, overlooks the obvious fact that "doctoring" is of recessive importance in health control, even in domesticated species and human beings. He overlooks also that the real determinants of disease mortality are the environment and the population, both of which are being "doctored" daily, for better or for worse, by gun and axe, and by fire and plow.

Pessimistic attitudes toward disease control are further accentuated by the extreme complexity of many of the disease mechanisms so far discovered. A better argument is that this very complexity increases the possible points of attack, one of which may some day be used for control measures.

History. Organized effort to understand and control game diseases is still in its infancy. The first known project was the British Grouse Investigation, on which a report was published in 1911.

The first American enterprises combining field and laboratory methods were Wetmore's (1919) investigation of lead poisoning in waterfowl, and the Ruffed Grouse Investigation sponsored by the American Game Protective Association in 1924 (Allen, 1924). The latter project is still under way.

Investigations of the "duck disease," undertaken by the Biological Survey and the University of California since 1918, have recently culminated in the discovery by Kalmbach (1930*a*) that Botulism is a cause, and probably the cause, of this important malady. A remedy for the duck disease—fresh water—was discovered long before its cause became known. Control works to regulate the water on the Bear River Marshes in Utah have now been installed by the Biological Survey.

In 1924 an outbreak of hoof-and-mouth disease in cattle spread to the deer in the Stanislaus National Forest, California, but was effectively stamped out by depopulating the area. This was our first venture in game-disease control.

A comprehensive investigation of quail diseases by various co-operating agencies formed a part of the Georgia Quail Investigation beginning in 1924. Their findings are published in Stoddard's book (1931, pp. 229–338). The Biological Survey is continuing work on quail at Richmond, Virginia, and is also studying diseases in other species. Certain quail diseases have been studied at the University of California (O'Roke, 1930).

An organized study of tularemia in wild life is now centred at the University of Minnesota (see publications of Green *et al.*) with the co-operation of the Spotted Fever Laboratory at Hamilton, Montana (Parker, 1929) and others. The U. S. Public Health Service is studying human aspects of tularemia (Simpson, 1929).

General studies of coccidiosis in game birds have been made by Tyzzer (1929) at Harvard, of bird parasites by Cram (1927) at the Bureau of Animal Industry.

The diseases of game predators and buffer species, and those affecting the agencies of transmission, are of course often just as important to game management as the diseases of the game itself, but are not here reviewed.

It need hardly be said that none of these direct attacks on the problems presented by particular game species or disease organisms are as yet complete. There are many others, some of which will be mentioned later, but the sum total of all the work to date is hardly greater than what should be done yearly during the next decade. It is particularly encouraging to note the active participation of medical schools and other institutions not directly charged with responsibility for wild-life conservation.

In addition to researches dealing with particular species or particular diseases of wild life, there is great need of interpreting the rôle of the disease factor in determining population density and its fluctuations. Until very recently such interpretations, for the game field at least, were entirely lacking. Without them there is a strong tendency for specialized investigations to run down blind alleys.

Elton's *Epidemic Diseases Among Wild Animals* (1931) and the Matamek Conference on Biological Cycles (1932) have, in one brief year, gone far toward filling this need. They offer the game manager at least hypotheses wherewith to visualize the disease factor in terms of population behavior.

Classes of Game Disease. Game diseases fall into various sets of categories.

They may be grouped, for instance, by the characters of their causative agents, or by their biological, geographic, or time distribution, or by the mechanisms which transmit them. The succeeding captions sketch roughly some of these groupings, and give examples of some of the more important.

Causative Agents. Game disease may have as its causative agent various living organisms, various nutritional deficiencies, chemical poisons, mechanical injuries, or *combinations* of these. The causative agents fall into eight groups:

1. *Virus.* Viruses are submicroscopic infectious agents. The "organism" is known to be capable of rapid multiplication, but only in living tissue. Whether it is a living animal or plant, or a chemical phenomenon, is as yet unknown. The latest indication is that a virus is a broken-down form of bacterial organism, disassembled, as it were, but nevertheless alive. Some viruses pass through the finest filters; others do not. This indicates a difference in size. The hoof-and-mouth disease of the hoofed mammals, for instance, is a filtrable virus.

2. *Bacterial.* Bacteria are microscopic plants some species of which infect the blood or tissues and secrete toxic waste products. Tularemia, for instance, is a disease of certain game, predators, and buffer species caused by a bacterium.

3. *Protozoan.* Protozoa are microscopic animals some species of which are parasitic in various body parts, often in the blood cells or in the cells of membranes. Coccidiosis, for instance, is a protozoan disease of gallinaceous birds and rabbits caused by various species of *Eimeria* which parasitize the membranes of the intestinal tract.

4. *Fungous.* Aspergillosis is a disease caused by the common fungus *Aspergillus fumigatus*, which develops in the respiratory system. Handley (Stoddard, p. 329) found it in captive quail, and Allen and Gross (1926) in ruffed grouse. The nature of the infection has been studied by Henrici (1930).

5. *Nutritional Deficiencies.* Captive game birds develop rickets and other "deficiency diseases" when their ration is lacking in vitamins or minerals. Whether wild birds do so is not known, but it seems probable that deficiencies sufficient to affect vigor or reproduction may account for some unexplained differences in productivity (see Food chapter).

6. *Gross Parasites.* Various large internal parasites inhabit the body tissues or body cavities of animals during all or part of their life cycle. Another group inhabits the external plumage or pelage, or attach themselves to the skin. Single species of parasites are commonly confined to a single species of host, or a closely related group of host species. Many, however, pass successive stages of their life cycle in successive and quite unrelated host species, called intermediate hosts. Predators are often intermediate hosts for the parasites of the game on which they feed.

For example: The roundworm, *Ascaridia lineata*, is an internal parasite passing its whole life within a single host. It infests grouse and poultry (Gross, 1930*a*) and sometimes invades the body cavity as well as the intestines. On the other hand, *Dispharynx spiralis* is an internal parasite passing its adult stage in the proventriculus and gizzard of gallinaceous and other birds, and its larval stage (Cram, 1927) in the pill-bug. The life-cycle is completed when the grouse eats the pill-bug. Allen (1924) found grown grouse apparently killed by the parasite.

Bird lice are external parasites passing their whole life upon a single species of host. Each host species commonly has its own species of louse. In weakened or incubating birds, lice may become serious.

Hippoboscid flies are external parasites of birds. One species contracts and presumably transmits the protozoan blood disease of California quail discovered by O'Roke (1930).

External parasites are frequently carriers of virus, bacterial or protozoan disease. Some contract and are injured by the disease, others merely mechanically transmit the infection, others harbor the organism but are not injured by it. Thus the rabbit tick is a carrier of tularemia, but is not itself affected adversely by the disease. Mild or even fairly heavy infestation with gross parasites does not necessarily produce a pathological condition in game.

7. *Chemical Poisons.* Some plants and insects (see Chapter XI) are toxic to game, likewise many insecticides, rodent poisons, and some industrial materials. Lead shot are eaten by birds, especially waterfowl, evidently in place of grit, and when ground up in the gizzard, are poisonous (Wetmore, 1919).

8. *Mechanical Injuries.* Sharp particles eaten as food sometimes puncture the crop or irritate the food canals. Thus oats irritate the food canal of red grouse (*Grouse Report*, p. 82). Spines of seeds were found by Stoddard (p. 128) to have punctured the crop of bobwhite, and in one case, caterpillar spines had punctured the cæcum. Seeds of coffeeweed killed an experimental quail, but whether by mechanical or chemical action could not be determined. O'Roke found a pheasant dead of hemorrhage caused by a large chestnut lodged in the crop.

9. *Combinations.* An astonishing multiplicity of interactions occurs among the eight groups of causative agents of disease, and the various factors of productivity. Thus elk die of infection

with *Bacillus necrophorus*, the organism gaining entrance through mouth lesions caused mechanically through eating the sharp spines or awns of squirrel-tail grass (Murie, 1930, p. 220). At least a part of the winter losses of elk in Jackson's Hole, formerly attributed to starvation, are in fact caused by this disease. The control of the objectionable grass, at least in the hayfields from which the elk are fed, at once suggests itself as a remedy.

Botulism is a chemical poisoning due to substances liberated by the action of *Clostridium botulinus* on certain foods. The poison appears to open the way for the entrance of the bacterium as well.

Screw worms infect mechanical injuries of deer and cattle, and sometimes cause death. In Texas, deer of all ages are said to die of screw worms if there is no deep water in which the animal can stand to drown the worms.

A cæcum worm of quail, Heterakis, is considered by Cram (Stoddard, p. 245) as a probable carrier of blackhead to quail, inasmuch as one of the two species found in quail is known to transmit blackhead to chickens and turkeys. Transmission is probably accomplished by blackhead gaining entrance through injuries to the membranes by the worm. The infection is carried to new hosts on the worm's eggs. Evidence of a similar association between Heterakis and blackhead was noted by Gross (1930*a*) in pinnated grouse and heath hen. A parasite which thus transmits another organism is called a vector.

Coccidiosis may be a factor in and may precipitate nutritional deficiency. Tyzzer (1929) found that chickens infected with it developed rickets, when similar but uninfected stock kept under the same conditions did not.

Ticks are known to transmit blood parasites and diseases of chickens, and may do so in game. The rabbit tick is known to be a carrier of tularemia among rabbits, and is suspected of transferring the disease from rabbits to grouse. Tularemia also occurs in the three species of wood tick (Green, 1931), which may prove to be vectors.

Hall (1931) states that the lungworm of mountain sheep (*Muellerius capillaris*) is carried by snails as an intermediate host. He suspects that mountain sheep in areas of igneous rock may eat snails for their calcium, and on the strength of this hypothesis recommends licks of ground bone and salt for certain areas where sheep have been suffering from lungworm and also, apparently, from a calcium deficiency, as attested by their eating the bones of old carcasses. Here, in short, is an apparent interaction between parasitism and the "special factor" of calcium.

Distribution in Space and Time. Presumably most diseases of game have the same geographic distribution as their host, or as their transmitting agent, or as their intermediate host. Some are readily transplanted, however, to new hosts and new ranges. Thus many game diseases have been derived from exotic livestock or poultry. The evidence so far available, for example, indicates that the ruffed grouse of the Canadian Labrador have none of the poultry parasites common to the ruffed grouse of New England and the Lake States (Gross, unpublished). The mountain sheep and elk of the Rockies have sheep scabies, presumably derived from domestic sheep, although possibly vice versa (Hall, 1931), while in those of Alaska, this disease has not been reported. The hoof-and-mouth disease stamped out in the Stanislaus deer herd in California in 1924 was an importation derived from cattle, and might have spread over all or a part of the entire deer range. The menace of its reimportation from Europe is ever present.

The game cycle, already briefly described in Chapter III, is the principle phenomenon so far known with respect to incidence of disease in time. The causative agent of the American cycle is presumably some virus, bacterial, or protozoan disease, often accompanied by severe parasitism. The cycle in British grouse is so far considered to be caused by a cæcal parasite, *Trichostrongylus pergracilis*. The reasons for the periodicity in cycle diseases is still obscure, although some promising leads were developed at the Matamek Conference (1932).

Mechanisms of Transmission. Any discussion of transmission must emphasize at the outset that many diseases are known but their mode of transmission is still unknown; also that some diseases do not require transmission, in the sense of communicating a new infection to a population hitherto free. They are there to begin with, and mortality is a matter of varying virulence rather than presence or absence of the organism. Even such endemic diseases, of course, require transmission in the sense of communicating an infection from one individual or generation to another.

As nearly as so far known, no diseases of game are transmitted within the egg, *i. e.*, they are not inherited in any genetic sense. Some, however, may be transmitted *on* the egg. Some nutritional deficiencies are now believed to be affected by inheritance, in the sense that the egg appears to carry reserves of vitamins sufficient to supply the offspring for some time.

Direct contact of parents and young is of course a common mode of transmission between generations.

Transmission of bacterial and protozoan diseases by gross parasites, internal and external, and by biting insects, has already been mentioned.

Transmission on the food is a very common mechanism. Thus the larvæ of the strongyle worm of red grouse, after hatching from an egg in the grouse feces, climbs a heather stalk in the presence of dew, encysts itself, is ingested by the grouse with the heather as food, resists the grinding action of the gizzard by its strong covering, and thus again reaches its final destination in the cæcum of the grouse.

Transmission on vegetable food is a common mode of transmission of parasites of grazing mammals. Thus the bladder-worm causing *Cysticerosis* of deer seems to be an early stage of a tapeworm of coyotes (Hall, 1931). The deer doubtless eats forage contaminated by the coyote feces, and the "round trip" is completed when the coyote eats the deer. Predator control is the most evident means of disease control in this case. Bladder worms of rabbits are likewise transmitted through dogs, the dog eating the rabbit and in turn contaminating the rabbits' food with his feces.

Transmission via animal food is also common. Insects eaten as food are often the intermediate hosts of parasites of insect-eating game birds, and rodents of the parasites of rodent-eating predators.

Biological Distribution of Diseases. The need for synthesis of our accumulated detail into a coherent picture of the disease factor, already mentioned in a previous caption, is further supported by the absence of any literature on the general biological distribution of typical diseases in wild life.

Tularemia, for instance, occurs in certain wild quail, grouse, rabbits, hares, squirrels, and mice. By artificial inoculation certain partridges, ducks, and wolves contracted it, but turkeys, pheasants, pigeons, and foxes did not. It occurs in captive sheep and cats. This distribution is exceptionally wide in both the number and diversity of hosts. Most disease organisms are common to a much narrower range of species. Some, as already noted, occur in a single species only.

Spread Patterns. Diseases, in general, fall into one or the other of two sharply different classes: (1) those which are normally present in the population at all times, but which are virulent in one time or place but not virulent in another; (2) those which are not normally present, but are usually virulent when they do occur.

Mortality from the first class of diseases obviously does not depend on reinfection from outside sources, but rather on variations in virulence alone.

Mortality from the second class of diseases depends on the actual spread of new infection. Imported or exotic diseases are of the second class.

When mortality dates from the first class of disease are plotted on a map, they commonly show no perceptible "pattern." In the second class, mortality is likely to show a zonal pattern concentric to the centre of infection, or a pattern suggesting the agency of transmission. Thus the *Game Survey* (p. 145) compiled a map of Wisconsin showing the incidence of mortality in the last grouse cycle, and found no zones, but rather a "moth-eaten" pattern of incidence. On the other hand, an outbreak like the foot-and-mouth disease in California deer, consisting of a new infection derived from cattle, would doubtless show a zonal pattern more or less concentric to the points of contact with infected cattle. Spread patterns are often of diagnostic value in preliminary determinations of the nature of an unknown disease. Determination of spread pattern exemplifies the kind of work which the unspecialized game manager can do as well or better than the specialist, provided the latter has told him what to look for.

Virulence and Immunity. The incidence of disease in species, space, and time cannot be dissociated from variations in its virulence, in the proportion of immune individuals, and consequent variations in mortality.

Any discussion of virulence and immunity in wild life must begin with the assertion that the laboratory method has partially exploded two fundamental assumptions which for many years confused our thinking on wild-life diseases.

One of these assumptions was that all wild animals, being rigorously selected by competition, were "healthy" and therefore not subject to disease, except upon the intervention of some predisposing cause. In some of the most important bacterial diseases, at least, this assumption must now be discarded. Resistance to such diseases is not a matter of health, but of immunity acquired by a mild previous attack. Perfectly healthy individuals without such immunity are apparently stricken with the same ease as imperfect ones.

On the other hand, in considering the severity of infestation by gross parasites, the old theory of predisposing causes probably still holds water.

The other assumption was that the presence or absence of mortality depended on the presence or absence of infection. In instance after instance, this assumption has had to give way to evidence showing infection to be always present, the variable being not its distribution, but again its killing power, as determined by its virulence and by the immunity of the host.

Both of these assertions reduce to the same common denominator: virulence is the fundamental variable in bacterial and probably also in virus diseases.

A given bacterial disease may show a widely varying virulence depending on the "strain" of the organism. Thus Green has found non-virulent strains of tularemia, and Parker and Spencer (1925–26) non-virulent strains of spotted fever. In the former case virulence seems to vary with time, the virulence being greatest at the peak of the cycle, and falling off after the population has been reduced to a point where rapid transmission is no longer possible. In the latter case, there is a strong indication that variations in virulence are geographic. The Bitterroot Valley strain of spotted fever seems always virulent; in some regions the strains now known appear usually non-virulent.

In general, virulence in all diseases increases when the infection is passed rapidly through a succession of susceptible hosts, and decreases when it passes slowly through hosts more or less immune or resistant.

Cyclic mortality and epizootics in general probably occur when the population consists largely of susceptible individuals born since the last-preceding period of mortality. This is about the same thing as saying that epizootics occur where dense populations offer virulence a chance to "step up" by quick transmission.

Green (Matamek Conference, 1932) has now advanced the significant hypothesis (for tularemia) that the immunes which survive the "crash" of a cycle are individuals which were born during the preceding period of low population, and which recovered due to the low virulence then prevailing. This hypothesis implies that during the period of high virulence few or no cases recover.

There remains the question of why, if tularemia or any similar disease is the causative agent of the cycle, the virulence should vary almost synchronously over the major part of the continent. To explain this, it is necessary to postulate some additional determinant of virulence, over and above the speed of transmission already mentioned. It is possible that some condition of light, or weather, or some electro-magnetic phenomenon, is the additional determinant of virulence (Matamek Conference).

Determinants of Disease Mortality. The foregoing sketch of the behavior of game diseases is offered simply as an explanatory basis for what the game manager is interested in, namely, the conditions of game and environment which determine freedom from disease.

A high density of population—the very thing the game manager is so far usually seeking to obtain—must be set down as the most fundamental condition favorable to disease. High density obviously speeds up transmission and thus increases the virulence of bacterial diseases, and also facilitates the spread of gross parasites and protozoan infections.

In its more advanced stages, game management is in effect the art of maintaining a population which is vigorous and healthy in spite of its density. Game farming, in particular, deals with an abnormal and unnatural population density. Domesticated animals are doubtless those species combining useful characters with the ability—original or acquired—to survive great or abnormal density. It is significant that no grouse, for instance, has been domesticated. Nevertheless management is applied to European grouse with great success, but with great care not to exceed a certain critical density (Leopold and Ball, 1931*a*).

Vigor and resistance in the game population frequently hark back to environmental conditions. Thus over-control of predators may allow the survival of weak or defective individuals and thus deteriorate vigor. Bad weather or under-control of predators may destroy the early nests and thus increase the proportion of "squealers" or unduly young individuals, and these, by wintering badly, may threaten the health of the whole population. The British, as already mentioned, seek to shoot off unduly young birds for this reason. Overhunting, by reducing the prime bucks, may delay or prolong the rut, spread the fawning into the summer, and accentuate winter losses from disease or starvation. Fritz, in his chapter of "The Pennsylvania Deer Problem," suggests that something like this happened in Pennsylvania deer. These are simply a few examples of a probable large number of interactions between the vigor or resistance of game and its environment, most of which are as yet unknown.

We come now to environmental determinants of disease. Density or abundance of transmitting agents and alternate hosts is, of course, a potent determining condition. Their predators, their food, and the weather in turn determine this.

Contact with domestic animals is of obvious importance in all diseases shared with or carried by them.

The planting of game-stock-bearing diseases acquired in game farms, or in other regions, or in transit, is on all fours with poultry contacts.

The dispersion of game food and cover is probably of great importance in all diseases where ease of transmission from one individual to another affects either the virulence of the disease or its distribution. The greater the dispersion of food and cover, the less the necessity for contacts. In red grouse management, for instance, snow is dragged from *fresh* heather, unpolluted by previous concentrations of birds, as a combined winter-feeding and disease-control measure. Disease control is always a good reason for giving each unit of population *several* places, instead of only one place, to feed, rest, dust, water, etc. More knowledge may show that it is bad practice to concentrate game at feeding stations, when the same result can be secured with fewer contacts by means of large food-patches or through encouraging the growth of natural food.

Many determinants of disease mortality are strongly and some are principally influenced by weather. It has long been claimed that cyclic mortality in grouse starts in cold wet years. It remains to be seen whether this is cause and effect, or two effects both arising from some common cause. The success of gray or Hungarian partridge management in England is unanimously thought of in terms of weather. Stoddard finds moderately dry seasons best for quail. DeLury (1930) suspects that game cycles are caused by sunspot variations and the corresponding variation in solar radiation and weather.

Types of Disease-Control. It is obvious even to the layman that control of disease by medication of wild game is impossible. Hence, as already stated, many laymen doubt whether the study of game diseases serves any useful purpose. They fail to appreciate that game management can control game populations and, to a certain extent, game environments, and that many controls can be effected through these means, once the necessary facts about the nature and operation of disease become known. The history of plant and animal diseases in agriculture shows that with enough facts, some vulnerable point eventually shows up at which each disease can be successfully combated.

A good example is found in the control works now under construction at the mouth of Bear River in Utah to reduce mortality from duck sickness. This disease was known to be associated in some manner with the lack of fresh water, even before its cause (Botulism) was discovered. Accordingly a dike is being thrown up to impound the discharge of the Bear River, and prevent its mixture with the water of Great Salt Lake. This impounded fresh water will spread over the marshes and undoubtedly reduce future losses. In short, the right kind of environmental control can reduce the mortality from duck sickness, which without control is alleged to have exceeded one million ducks during the worst years.

Many manipulations of the environment will suggest themselves as disease controls, once sufficient facts become available. Control of the quality and distribution of winter food in British grouse has already been mentioned. Control of squirrel-tail grass on the winter elk range is being accomplished by fencing and cutting out the spots where this grass grows.

Another type of game disease control is the temporary removal of the whole game population to prevent the spread of new infections. It was successfully used in stamping out the hoof-and-mouth disease in California. About 22,000 deer were killed on 1142 square miles. A virtually complete clean-up resulted. The depopulated area started to "fill in" as soon as the work had been finished, but the former density is not yet re-established.

Another type of control is the selective removal of susceptible classes of individuals. The effort to shoot off too-young grouse in Britain, and the reasons for it, have already been mentioned. This represents actual practice on assumed but unproved grounds.

The controlled use of fire, which Stoddard suspects may reduce some insect parasites of quail in the South, may prove to be, in some regions, a means of range sanitation on lands devoted primarily to game. Use of fire without sound evidence of its effects, or on lands primarily devoted to other crops, is of course to be deplored.

Attacking the carriers or intermediate hosts of game disease at some vulnerable point will doubtless be used as a type of control in the future, but no actual instances of its practice are as yet known.

The most powerful tool of all, but one as yet not even theoretically developed, is the artificial immunization of individuals by the propagation and spread of mild strains of disease. It is too early to speculate on its future utility.

Effects of Disease on Predator and Sex Ratios. It has long been recognized that any reduction of game population density through disease increases the predator-game ratio and also changes the relative abundance of predator foods. Thus when disease decimates the northern rabbits, there are less rabbits per predator, and grouse become relatively more available than rabbits. The resultant drain on grouse was long supposed to be the cause of grouse shortage. The effect may be either way, depending on which species first becomes diseased. The converse occurred in 1929, a high mouse year, in Wisconsin. Foxes, house cats, and raptors lived almost entirely on mice, except when the winter snows temporarily protected the mouse crop. By 1930 the mice were much scarcer, and predators fell back on rabbits, and to some extent other game.

Another important but unexplored secondary effect of disease is differential mortality as between sexes, with a consequent disturbance of the sex ratio. How serious such a disturbance may be can be inferred from the Australian scheme of exterminating rabbits by trapping females only in enclosed tracts. The resulting excess of males is said to reduce productivity to the point of exterminating the enclosed population.

Quail confined at the Clinton Game School lost more hens than cocks from unidentified causes, possibly disease. During two bad years for mallards, presumably due to disease, there was an excess of drakes in the school flocks. Quail confined by Stoddard in Georgia lost more hens than cocks from coccidiosis. O'Roke found that the heaviest loss from *Hæmoproteus* in California quail was in hens after they had nested. On the other hand, various native and exotic ducks confined by Wm. P. Steele at Sedalia, Missouri, lost drakes more readily than hens, especially in the Chinese Mandarin duck and in all the teals. It is possible that the heavy preponderance of drakes found by Lincoln to obtain in wild ducks all over the continent will be traced in part to differential sex mortality from duck disease and lead poisoning. Lead poisoning in at least some instances operates against the males (Wetmore, 1919). Lead has another effect in causing abortion in mammals and infertile eggs in birds (Cole, 1915).

The evidence so far available indicates that necrotic stomatitis in elk, already referred to, operates against the males, but this is not yet certain.

The differential effect of cyclic mortality on sexes of ruffed grouse was recognized as early as 1906. Forbush (1912) says the kill in Massachusetts ran heavily to cocks in both 1906 and 1907, the latter being the year of heaviest mortality, and the ratio did not resume normality until 1908. Many disturbances have been reported in conjunction with later cycles, always in the direction of hen shortage. It was at first assumed that the hardships of incubation subjected the adult hen to disease and enemies, and that this alone was responsible. The more recent idea of differential mortality from disease affecting the whole population seems a more satisfactory explanation for the apparently sudden change in sex ratio. The Wisconsin Prairie Chicken Investigation is now finding evidence of a hen shortage, several years after the cycle of 1927 has passed.

Any marked disturbance of the sex ratio may be considered as circumstantial evidence of disease, unless some other "visible" form of differential mortality can be adduced to explain it.

Summary. Disease not only kills game but also its predators and buffers. Disease may affect distribution, density, sex ratio, and fertility.

Disease control is a matter of doctoring the environment, not the animal.

TABLE 43

SOME PUBLICATIONS ON GAME DISEASE

Subject	Author	Date	Specifications
Bobwhite	Stoddard	1931	General, incl. captives
Valley Quail	O'Roke	1930	Protozoan, California
	McLean	1930, p. 55	Brief review
Ruffed Grouse	Allen	Series, 1924-1931	
	Gross	Series, 1925-1930	
	Tyzzer	1930	Flagellate parasites
Red Grouse	Grouse Report	1911	Strongylosis, etc., Britain
Prairie Chickens	Gross	1930b	Mostly parasites, Wisconsin
Heath Hen	Gross	1928c	Monograph, incl. parasites, Mass.
Waterfowl	Riley	1931	Sarcocystis, a flesh parasite, Minn.
	O'Roke	1928	Intestinal parasites, California
	Wetmore	1918	Duck sickness, Utah
	Kalmbach	1930a, 1932	Botulism as cause of duck sickness
	Hobmaier	1932	Botulism & its control, California
Rabbits	Schwartz & Shook	1928	Parasites & diseases of domestic
Deer	Hall	1927	Parasites & epidemics, California
	Van Roekel	1929a	Parasites, California
Antelope	Skinner	1924, p. 20	Brief list, Yellowstone
Elk	Murie	1930, 1932	Necrotic stomatitis, Wyoming
	Rush	1932	Bang's Disease, Yellowstone
Mountain Sheep	Rush	1928	History of epidemics in Northwest
	Hall	1931	Scabies
Epidemics	Elton	1931	General review
	Matamek Conference	1932	As causing cycles
Parasite Control	Hall	1931	In big game
Bird Parasites	Cram	1927	Nematodes, Strongylata, Spirurata
Tularemia	Green et al	Series, 1928-1931	In hares and grouse
	Parker and Davis	1932	Tick transmission. In sage hens
	Simpson	1929	In humans
	Parker	1929	In quail
	Barnes	1928	Semi-popular
Lead Poisoning	Wetmore	1919	In waterfowl
	Magath	1931	Minnesota
Foot and Mouth	Mohler	1926	Outbreaks in livestock
Coccidiosis	Tyzzer	1929	In gallinaceous birds
Game Farms	Van Roekel	1929	California

This is a fragmentary table. It omits work on predator and buffer species, and is by no means exhaustive, even for the species and other headings which are included. The lists of references appearing in an item here cited will often suggest what other items to run down. The items opposite species do not repeat those under other headings, nor vice versa. For the full reference on any item consult the author's name and the year in the main bibliography. (See Appendix.)

Investigations of particular diseases have outstripped interpretations of the rôle of diseases as a factor.

Disease is caused by viruses, bacteria, protozoa, fungi, nutritional deficiencies, parasites, poisons, mechanical injuries, and combinations of these agents.

Distribution varies in both space and time. Transmission is accomplished on the egg, by contact, by food, and by vectors. In some bacterial and virus diseases, varying virulence determines mortality, rather than the fitness of the host. New infections can be distinguished from endemic diseases by their zonal spread-patterns. Density of transmitting agents and alternate hosts, contacts with domestic animals, dispersion of food and cover, and weather affect disease. Some of these can be controlled. Local extermination, selective removal of individuals, fire, and immunization also offer possible means of control.

It should be remarked in closing this chapter that if the reader has not emerged with a clear picture of game diseases, he is no different from even the most skilled specialists, and need berate neither himself nor the book. If, however, he has built up an enlarged appreciation of the scope and complexity of the disease factor, and has caught a few convincing glimpses of its hidden mechanisms, the writer's object will have been accomplished.

We pass now to accidents, the last category of "the slings and arrows of outrageous fortune."

Chapter XIV

ACCIDENTS

Definition. Accident mortality includes all loss from physical causes alone, as distinguished from losses from other living organisms (such as diseases, parasites, hunting, or predators), from chemical causes (such as poisoning), from welfare factors (such as food, cover, and water), or from mechanical causes combining with diseases.

Weather losses associated with food or water shortage or disease are not here classified as "accidents," because it is very seldom that weather is anything but a contributing influence to such mortality. If healthy well-fed individuals of any given species were not able to resist the worst weather normally occurring in its geographic range, then its range would long ago have shrunk to what the species can endure. For this reason weather mortality associated with these other factors is ascribed to them and not to weather, and has already been treated.

Weather losses *not* associated with these other factors are here treated as coming under the category of "accidents."

Importance of Accidents. In game birds, five sources of accident mortality seem far to exceed all the others in importance. These are, (1) burning of nests or young in forest or marsh fires, (2) drowning of nests or young in floods, (3) destruction of nests by agricultural machinery, (4) imprisonment of ground-roosting birds under snow, (5) waterfowl destruction by oil. Of these five kinds of accidents, 1, 3, and 5 are unfortunately the only ones susceptible of any important degree of control.

In game mammals it is far less clear whether any particular kind of accident is outstanding, or whether all of them are collectively as important as in birds.

In constructing "life-equations" or gain and loss tables such as suggested in Chapter VII, accident mortality should not be overlooked, even though it is not visible and cannot be assigned a definite value. There is in all wild life a large variety of miscellaneous accidents no one of which is of outstanding importance, but which collectively take a much larger toll than is ordinarily supposed. Many of these occur only in certain species or groups.

Accident mortality, like disease mortality, is seldom observed, and for the same reason that disease is seldom observed, namely: the injured individuals either hide and die, or they are consumed so promptly that their demise is not noticed, or their death is ascribed to other causes.

Biological Distribution of Accidents. Certain kinds of accidents, such as burning of nests or young, occur in practically all species of game, and all predators except those denning underground. The frequency of occurrence, however, certainly varies considerably between species and between localities.

Another class of accidents is peculiar to certain groups. Thus locked horns are for obvious reasons peculiar to the males of antlered game. Electrocution by transmission lines is confined to hawks, eagles, and herons, these being the only birds accustomed to alight on poles and capable of short-circuiting the conductors by the timely release of their stringy, semi-liquid excrement (see Michener, 1928). Mudballs on the feet are confined to gallinaceous birds like Hungarian partridges, which frequent fields of heavy soil after light rains. Blowing down of nests is confined to doves, because no other game bird builds a flimsy nest in a tree. Falling off cliffs is probably confined to deer when they are blinded by pink-eye (Hall, 1927), or when the rutting males are in combat.

Lastly, there is an aggregation of miscellaneous accidents concerning which information is too meagre to assign them as peculiar to any particular group. Table 44 attempts to classify accident mortality, but undoubtedly omits many causes of accidental death.

Certain alleged accidents, such as addling of eggs by thunder, lightning, or explosions, are not yet accepted as scientific fact, in spite of the wide credence accorded them in traditional lore. If eggs are addled by these disturbances, it is probably only in certain stages of incubation. Lightning, of course, electrocutes many kinds of game, including flying birds (Sugden, 1930).

The very oddity of some of the fates that game is heir to suggests that neither the variety nor the extent of accidental deaths is yet fully appreciated. The drama of accidents in nature is perhaps more real to us than the drama of tooth and claw, because its counterpart in human accidents is still to be seen on any street corner, whereas human depredation has become, by

TABLE 44

BIOLOGICAL DISTRIBUTION OF

(Important causes underlined. Authority is quoted only in cases which might other-

	Known Instances
A. ACCIDENTS COMMON TO MANY OR DIVERSE SPECIES	
*<u>Burning of nests or young in forest & marsh fires</u>	All species
<u>Drowning of nests or young in heavy rain or floods</u>	Nearly all birds
Drowning during flights over water	Bobwhite, pheasant, Hungarian, many migrants
Burning or suffocation of adults in forest and marsh fires	All species to some extent
Hit by motors	Ringnecks, grouse, quail, deer, woodcock, rabbits, skunks, etc. (Fly-catching & nocturnal species & fighting males.)
[x]Eggs addled by electrical storms (?)	[x]All birds, especially geese
Caught in steel traps	All small game
B. ACCIDENTS PECULIAR TO CERTAIN GROUPS	
*<u>Incubating birds or nests destroyed by mowing machines</u>	Quails, pheasants, ducks, Hungarians
<u>Crusted over while roosting on snow, or imprisoned by sleet on vegetation</u>	Quail, Hungarian, rabbit
<u>Crusted over after diving under snow to roost</u>	Ruffed grouse
*<u>Oil on feathers or fur</u>	Waterfowl, beaver (Phillips & Lincoln, 1930)
Drowning in steep ditches	Young of gallinaceous group
Breaking through ice and drowning	Elk
Freezing to the ground while roosting	[x]Pheasant, ruffed grouse (?)
Strangulation by ice on head	Pheasant (Beyers, 1932)
Freezing of eggs	Red grouse (Scotland)
Tail freezing to ground	Cock pheasant
Feet and feathers freezing to ice	Ducks
Snowballs on tail	Pheasant (Wight, unpubl.)
Goring by horns	Elk (Murie, 1930)
Locked horns	Deer, elk, moose
Flying into lighthouse & other lights at night	Ducks

[x] Not yet established by scientific evidence.
* Subject to control in some degree.

TABLE 44

ACCIDENT MORTALITY IN GAME

wise seem improbable, or where an especially good description is available.)

	Known Instances
Flying into white buildings and windows	Ruffed grouse, bobwhite
*Electrocution by transmission lines	Hawks, herons (Michener, 1928)
Miring in bogs	Elk, buffalo, young ducks
Mudballs on feet	Hungarian partridge (England); Mich. (Yeatter, unpubl.)
Falling off cliffs	Mule Deer
Carried over waterfalls	Swans (Niagara)
Flying into high bridges	Ducks
Flying into woven wire fences & backstops of tennis courts	Bobwhite, pheasant, ruffed grouse, Hungarian
Freezing after wetting plumage on fermenting manure	Bobwhite (Errington, 1930a)
Wedged between trees after jumping down a bank	Deer
Leg caught in fork while browsing	Deer (Russ, 1931)
Blowing down of nests by wind	Doves, herons
C. MISCELLANEOUS ACCIDENTS	
Electrocution by lightning	Deer, pelican, ducks
Flying into overhead wires	Pinnated grouse, Hungarian, bobwhite, Wilson snipe
Bruised by flying against solid objects	Bobwhite, ruffed grouse
*Gassed in orchard fumigation	California quail (True, 1931)
Feet caught in wire fences	Mule deer, whitetail deer
Feet wedged in brush	Mule deer fawn
Impaled on splinters	Deer, bobwhite
Ice balls on plumage	Bobwhite (Mo.)
[x]Killed by hailstones	Bobwhite ? ducks? herons
*Falling into concrete aqueducts	Deer (Calif.)
Young falling into ditches, crevices & plow-furrows	Bobwhite, red grouse (Scotland)
Head caught in suspension wires of overhead cable	Sora Rail
Anus blocked by burdocks on fur	Cottontail (Errington, unpubl.)
[x]Club feet due to freezing (?)	Blue Goose (McIlhenny, p. 305)
[x]Clam locked on head or neck	Coot, Wis.

sublimation, a relatively polite contest conducted for us vicariously by specialists with footballs, with check books, or, at intervals, with long-range rifles.

The factor of accidents in game should not be thought of as beyond control. Some of the heaviest tolls are entirely man-made or subject to our intervention. In the following captions the five most important classes, and some others of special interest, will be discussed from the control angle.

Fire Mortality. The influence of fire on game habitat has been discussed in the chapters on game and food and cover. There remains to be covered the direct mortality from fire as a component of the aggregate loss from accidents, and some general observations on the fire-relationships of game.

Fire's indirect influence on game range is undoubtedly more important than its direct casualties. All writers agree on this point. (See Clepper, 1931; Austin, 1930; Stoddard, p. 401; Leopold, 1923.)

Nevertheless the direct casualties may be very great. Any fire, however light, of course makes a clear sweep of all ground nests and helpless young. This loss of nests and young is undoubtedly the heaviest item in the direct mortality from fire. The peak of the fire season in most regions is the peak of the nesting and fawning season.

Even when fire occurs in advance of the nesting season, there is often some direct damage. Thus Schmidt (unpublished) observed that sharp-tail grouse, evicted by the great Wood County (Wisconsin) fire of 1930, returned to their blackened dancing grounds in the spring of 1931, but because of the complete absence of cover, did not nest and apparently could not nest until the new year's vegetation had made a start. Such delayed nesting represents a loss in quality and probably in quantity of the year's crop.

Some progress has been made in prevention and suppression of fire in timbered regions, but the promiscuous uncontrolled burning of marshes, grassland, and farm woodlots still goes merrily on, especially in our best breeding grounds for waterfowl and prairie chickens. Organized public effort to stop it is almost nonexistent. This disparity evidences the prevalent lack of co-ordination in our "conservation" departments. Fire control is regarded as the forester's job, and stops where the forest land stops, even in states where forestry activities are or have been supported by game revenues. There is no hesitation, however, in spending money to *restock* the deteriorated game ranges. Restocking is something the voters can understand.

There has been much unreliable romancing about the behavior of game in the presence of fire. Even so eminent a writer as Van Dyke (1904) asserts: "Let but the trail of smoke drift down the wind across the forest, and all the game for miles and miles will catch the signal for fear and flight." This implies an instinctive and immediate fear of smoke as such.

No such fear seems to exist. I have seen deer in New Mexico feeding peacefully within half a mile of a big fire that had been filling the woods with smoke for a week. I have seen where deer went to water across a burn on which the snags were still smoking, when they could just as well have gone around it. Stoddard has seen quail fly out of the way of an advancing fire with apparent unconcern. Doctor E. W. Nelson, former Chief of the Biological Survey, told me that he has seen deer on the White Mountain Indian Reservation in Arizona actually *seek refuge* in the smoke of fires from the torment of flies which infest that country in late spring. He says that the Apache Indians were accustomed actually *to set fires* during the fly season *for the purpose of decoying deer* to their ambushed hunters.

On the other hand, any number of unimpeachable authorities attest the stampeding and scorching or burning alive of adult game birds, mammals and predators in the presence of large fires, not only in this country (see Guthrie, 1928; Kipp, 1931; Leopold, 1923), but also in Siberia (Shostakovitch, 1925). How is this apparent contradiction to be explained?

Fire has always been part and parcel of the evolutionary background of our present species in most regions. Ordinarily they have no more fear of it than of thunder or windstorm. Occasionally, however, as many fire-fighters know to their cost, a fire does unexpected things. A slow-burning front may encounter some change of wind, temperature, slope, or fuel, and flare up in one sudden devastating blast of flame. More rarely a whole mountain or valley may virtually "explode." Foresters call this a "blow-up." On a fire of irregular front, these sudden changes may confuse or entrap even experienced woodsmen, so there is nothing surprising in their stampeding game. Even flying ducks have been brought down, presumably by some ascending blast of heat from a "blow-up."

Game may also stampede in the combined presence of fire and fire-fighting crews, whereas either operating alone would be evaded in the usual businesslike manner. This unaccustomed combination of alarms undoubtedly accounts for many recorded observations of game dashing into flames, or stampeding over burned ground still hot with snags and embers.

The large number of records of game dead of suffocation rather than burns, and of game taking refuge in water or meadows, support the hypothesis that game ordinarily evades fire in a cool and collected manner, but may at times be entrapped or stampeded when unexpected complications develop.

That the ordinary relations of fear and rapacity as between game and predators are suspended in the presence of severe fires is attested by plenty of reliable evidence.

Highly localized game, such as species with a "home range" of very short radius, or females with hidden nests or young, may not move freely to escape fire. The evidence even gives grounds for suspicion that unstampeded females may sometimes deliberately enter burning coverts containing their young. Free movement in the face of fire seems, however, to be the general rule. In large fires this may give rise to individual or mass migrations into new range (Shostakovitch, 1925).

While the popular mind as a rule overestimates game's fear of fire, it undoubtedly underestimates the fatal effect of even slight body burns. Any hoofed animal with scorched feet, for instance, is worse than dead. A crack quickly develops between the hoof and the hide, the crack becomes fly-blown, and that's that. Game going about on stumps of legs is a frequent aftermath of fire.

Crusting Snow and Sleet Mortality. The greater part of winter losses in game are caused by lack of food and cover. Predators or disease may do the actual killing, but as demonstrated by Errington (1930, 1931) in quail, and Murie (1930) in elk, their ability to kill usually harks back to poor or insufficient food.

Once in a while, extraordinary weather kills healthy well-fed game. Some "freak" forms of weather mortality are given in Table 44. These are too rare to merit discussion as important "leaks" in productivity. Mortality on a large scale, however, may occur through imprisonment of ground-roosting birds and rabbits by sleet or by crusted snow.

Ice-prisons form when the vegetation under which the birds are roosting is so completely iced by sleet as to form a rigid cage. Snow-prisons form when falling snow covers the roosting birds, and is later crusted by sleet during the same night. Neither is fatal if promptly thawed. Ice-prisons without snow probably never catch more than a fraction of the game population, because they form only in those accidental instances where the grass canopy over the roost is nearly complete. Snow-prisons, however, sometimes nearly wipe out the ground-roosting game over large areas. Bobwhite quail, Hungarian partridges, and rabbits have been found dead in both ice and snow prisons.

A special form of imprisonment occurs in ruffed grouse, which dive *into* the snow to roost, and hence can be caught by sleet alone, whereas in quail which roost *on* the snow, it is only the combination of snow followed by sleet which is dangerous. Prairie chickens also roost and tunnel under snow. Whether they enter by diving, or only by digging, I do not know. The total absence of reports of imprisonment of chickens under snow is worthy of note. This species, for this and other reasons already given, is probably the most weather-proof of our upland game.

All forms of direct imprisonment by snow and ice are beyond control, hence game management is concerned mainly with the question of how often dangerous conditions may be expected to occur. Their frequency is roughly proportional to the frequency of heavy sleets, so that it might appear that the risk as between any two localities could be determined by comparing their Weather Bureau records. These records, however, are too detailed—they record every drizzle of sleet no matter how insignificant, and sometimes fail to give the total thickness. The Game Survey (p. 75) found that telephone companies often keep records of the *diameter* of sleet coatings formed on their wires. Such records afford a very practical index to thickness of sleet on snow and vegetation, which is in turn an index to the frequency of game-killing sleets.

The Game Survey found that quail-killing winters in the north central region are spotty in geographic incidence, but in any one spot may be expected every four to seven years. This frequency of course is a combination of starvation and weather losses.

Grouse-killing winters are much farther apart, because starvation is averted by budding.

Drowning of Nests. The only other wholesale mortality from weather is the desertion or destruction of nests flooded by heavy rains or high water.

Nesting on ground subject to overflow can sometimes be prevented by burning off the nesting cover. Flooding by rains is beyond control, so that all the game manager can do is know his risk, *i. e.,* know how often he must expect losses and how big they will be.

All gallinaceous bird nests are built in a cup or hollow, usually excavated by the hen. The function of the cup is evidently to prevent rolling away of eggs and to retard evaporation. A splashing rain is more likely to flood this cup if it occurs before incubation than if it occurs during incubation, when the cup is "roofed" by the sitting hen. Possibly this is one reason why a pre-incubation rain seems to cause more desertions than later rains. A more powerful reason is doubtless the decreased willingness to desert as incubation advances.

The frequency of rain-broken nests is, of course, a matter of terrain and rainfall. Hilly or light land loses fewer nests than flat or heavy. Drowning of nests is most serious where a heavy predator population retards successful re-nestings, or where it has prevented the successful hatching of early nests so that the year's crop depends wholly on the re-nestings which the rain destroys. Stoddard (p. 347) observed an actual case of this interaction between rain and predators. The wet summer of 1928 was followed by a poor or spotty crop with many "squealers" on most preserves, but on one in which nest-predator control had been particularly thorough, an abundant crop was obtained.

Oil Mortality. A sobering example of the price of economic "progress" is found in the wholesale spread of oil pollution during the last two decades.

Phillips and Lincoln (1930) thus describe its effects on waterfowl:

"When birds alight on an oil-covered water surface, they soon find their feathers saturated with the oil and are unable to again take flight. The fine down which insulates their bodies against cold and water becomes matted and water-soaked . . . so that the birds perish from cold and hunger, while in some instances they are actually drowned. Live birds in this oil and water-soaked condition have been rescued, washed clean with soap and water, dried out, and liberated without suffering any apparent ill-effects, but unless human aid is rendered, birds that alight in an oil-covered water area are almost certainly doomed to death."

Waste oils or oily mixtures are discharged by ships, industrial plants, railways, city sewers, and oil wells in both inland and coastal waters. Lincoln (1930*a*) says that 5500 tons of heavy oil are released yearly near New York Bay from the discharge of ballast water alone.

A single experimental discharge of 7000 pounds of fuel oil (1/1500 of New York's yearly dosage of ballast oil) was released and measured by the Bureau of Standards. It "filmed out" over 900 square miles of water surface in several days. No form of trap or poison deliberately set out for the destruction of aquatic wild life could compare with an oil-film.

Oil pollution is theoretically entirely controllable, and Congress in 1924 passed an "Oil Pollution Act." However, ships are so mobile, and the discharge of oil from sewers is determined by so many thousands of people, that it may be doubted whether any force but inherent decency can do more than mitigate the evil. The main hope is that oil hurts resort properties as well as birds. For property values we have a real respect.

Agricultural Machinery. Nest mortality from agricultural machinery is usually caused by desertion following the removal of cover, and is discussed in Chapter XII on cover control, and in Chapter XV under nesting studies. Not infrequently, however, the incubating hen is actually mangled or beheaded by mower, or the eggs are broken. Such cases classify, under the scheme we are here following, as accidents. A method of avoiding such accidents by detecting nests in fields of hay or small grain, and leaving "islands" of uncut hay or grain around each nest is depicted in Fig. 27.

The present methods of detecting nests are doubtless subject to great improvement. Until very recently no one has paid any attention to such problems. A true index to the temper of this mechanical age is the disparity between the infinite brains and effort devoted to the perfection of utilitarian machines, and infinitesimal attention to their sometimes ruinous effects on the merely beautiful aspects of the countryside.

Agricultural machinery casualties are a major leakage in farm-game productivity. There is no reason whatever for this leakage to continue indefinitely. Control of this factor is feasible. Many farmers would voluntarily save nests if they were given a device for automatically discovering them.

Roadway Accidents. Motor transportation has brought one conspicuous exception to the rule that accidental deaths go unnoticed. The killing of an animal by a motor car is usually noticed by its occupants, and if the body remains on the highway, by hundreds of subsequent cars. This unusual visibility gives rise to widespread alarm over the destruction in wild life wrought by cars, while other more destructive but invisible factors are at work but go unnoticed. Linsdale (1929) has analyzed this popular fallacy, and shown how ordinary country roads with brushy margins, banks, bridges, trees, and marshy ditches supply food, nesting grounds, shade, and water to wild life, and thus may do it much more good by improving its environment than harm by running over a part of the resulting population.

It should require no citation of authority, however, to show the game manager that the popular alarm over motor-killing of wild life on highways is exaggerated. If the reader has grasped the principles set forth in this volume, he can figure it out for himself. Let us take the cottontail rabbit, a frequent victim. The worst that a highway could do would be to exterminate, let us say in a year, the rabbits whose ranges it intersects. Table 22 gives the daily radius as ⅛–¼ mile. The yearly radius is unknown, but by analogy is hardly more than a mile. A high-speed highway, then, might conceivably wipe out annually the rabbits on a strip a mile wide. How far apart are high-speed highways? Usually there are only one or two per county, even in farm country. Allowing two in a county 20 miles wide would account for 10 per cent of its rabbits only. The actual probable loss is of course much less than these liberal assumptions would indicate.

A count of dead jackrabbits on a highway across Idaho showed an average of two per mile (Gordon, 1932). Assuming traces remained countable for two weeks and that the loss continued through half the year, this would indicate about 25 jacks killed per mile per year. If the radius is two miles, and the density a quarter of the lower figure indicated in Table 15 (one per acre), the population of the ranges intersected by the highway would be 300 rabbits per mile, of which 25, or 8 per cent, would be killed by cars.

While motor-killing of game on highways is believed to be ordinarily a minor "leakage" in productivity, there are occasional circumstances under which it becomes serious. An outstanding example is the night-killing of deer on motor highways *salted* to reduce dust. In 1929, 60 deer were thus killed on 25 miles of highway in Michigan,—over 2 deer per mile per year. In 1930 block salt of the kind used for cattle was put out by the Conservation Department to decoy the deer away from the road salt. The losses promptly fell to eight deer, or one-third deer per mile per year (1929–30 *Report*, p. 256).

A highway may be, in effect, "salted" for animals of special habit, such as the fly-catching redheaded woodpecker in mid-summer. It is "salted" with a special insect supply, a monotone background for their pursuit, and a clean "tablecloth" on which to catch and eat cripples.

Measurements of accident mortality which can be related to known units of population are very scarce. One such measurement is the nesting mortality from agricultural machinery described in Chapters XII and XV.

The Pennsylvania wardens estimate that 1898 deer were killed by motors and trains in that state in 1931. This loss was regarded as serious enough to warrant a public appeal to motorists by the governor. The estimate, in the case of so visible a form of mortality, is probably reasonably correct. Clepper (1931, p. 32) estimates the deer population of the state at 800,000. This is probably a much less accurate figure, but if we accept it, the percentage of loss from motors and trains would be a quarter of 1 per cent, a very small figure indeed.

A farmer in Iowa, who played host to a flock of some 50 prairie chickens, told me he picked up about a dozen birds per year under a high two-cable transmission line which bisected their range. This farmer made a special effort to keep track of this loss, and the clean highway under the wires, in conjunction with his own work in the adjacent fields, probably enabled him to get a good count. The flock was about stable. This transmission line, plus a few hayfield nests, might absorb the entire yearly increment from such a range.

Classifications of accident loss unrelated to specified population units are more common. Thus Lincoln (1932) compiled post-mortems on 2426 small land birds which were found dead and reported because they bore bands. His table, converted into our categories, indicates death from:

FACTOR		PER CENT OF TOTAL DEATHS
Shooting and traps		28
Predators (cats)		10
Starvation		1
Accidents:		
Windows, wires, entanglements	3	
Motors and trains	2	
Storms and freezing	3	
Drowning	1	
	9	9
Miscellaneous and unknown		52
Total		100

Education by and Recovery from Accidents. The Iowa Game Survey (1932) quotes old timers who after each stormy evening made it a practice to pick up gunny sacks full of prairie chickens under the telegraph lines when they were first projected across the prairies. The previous caption, on the other hand, described a flock living literally under a much deadlier obstruction, and sustaining only a tolerable loss therefrom. One cannot avoid the inference that some degree of "education," either individual or racial, accrues from the persistent incidence of some accidents in some species. Whether game birds will ever "learn" not to nest in hayfields is a more puzzling question because of the penalty being deferred until long after the act.

Injured individuals possibly recover from ordinary accidental wounds more readily than we suppose. Thus Austin (1931) says songbirds "released with broken wings soon were removed from nets [maintained for banding studies] into which they had flown." Equally astonishing is the evidence of successful re-uniting of broken wing, leg, and thigh bones found in wild red grouse (*Grouse Report*, pp. 162–164).

Summary. The outstanding causes of loss from accident in birds are fire, flood, agricultural machinery, imprisonment in snow, and oil.

Some accidents occur in diverse species, but some are peculiar to certain species. Forty-eight kinds are of record in Table 44.

Fire does not ordinarily stampede game. The loss of range and young is much more serious than burning of adults.

Ice and snow prisons form rarely, but are serious when they do.

Drowning of nests is more prevalent on heavy than light soils, on flat than hilly ground, and during oviposition than in incubation.

Oil pollution is serious, and the hope for effective remedies is remote.

Motor traffic is overrated as a game destroyer. Only when the game is "baited" does it become serious.

Animals sometimes recover from injuries, even broken wings.

Chapter XV

MISCELLANEOUS TECHNIQUES

ARTIFICIAL PROPAGATION

The fundamental difference between artificial and wild management has already been pointed out in Chapter II. General aspects of domestication and transplantation as properties of game have been presented in Chapter IV. There remain to be reviewed the techniques for accomplishing artificial propagation and for making plantings.

These techniques are numerous and varied, and are well covered in existing literature. Hencc no attempt will be made to present each of them in detail. This chapter will rather sketch functions and basic methods. A special bibliography by species is added, to put the reader in touch with the detailed literature.

Functions. One of the most indispensable functions of artificial rearing is to furnish gentle stock for experimental research. Many experiments necessary to answer questions about wild management cannot be satisfactorily performed on newly confined wild stock. The importance of good experimental stock will increase as researches enter upon the physiological field.

The importance of having artificially reared stock for "reseeding" coverts accidentally depleted by overshooting or hard winters is obvious, and needs no comment.

The high cost, as well as esthetic limitations of artificially reared birds, makes it doubtful whether such stock will ever become important for release as shootable game.

Rearing Techniques. There are two basic propagation techniques: (1) those in which the wild breeding potential of the species is artificially increased; (2) those in which it remains the same as in the wild.

The first is applicable only to birds. It breaks down the clutch limit by removing the eggs as they are laid, or it induces renesting by removing the clutch just before completion. In either case, by reason of some physiological reaction as yet unknown, the hen is thus induced to keep on laying indefinitely. Bobwhite hens have laid up to 128 fertile eggs in a season, pheasant hens up to 104, and mallards up to 40. As nearly as known, most birds which lay at all in captivity can be induced to lay in excess of the natural clutch by timely removal of eggs from the nest. For convenience, any technique which breaks down the clutch limit may be designated as an "excess egg" technique.

The second technique is used for mammals bred in captivity and also for birds when they are allowed to complete their natural clutch.

In practice, both techniques intergrade with wild management, and with each other. Thus a wild nest may be robbed for propagating eggs, either piecemeal or in toto. In either event a new clutch is likely to be completed and raised as a wild nest, while the eggs removed are available for artificial rearing. The only loss is the lesser age of the wild brood, and the risk that re-nesting may not follow.

Again wild birds may be wing-clipped and confined in a large pen containing natural vegetation, where they may nest and bring off a natural clutch. This latter technique is usually known as "semi-wild" rearing. It is used for species which do not lay freely in crowded quarters (Hungarian partridge) or which are liable to disease when crowded (grouse).

Again a wild clutch may be taken at the beginning of incubation, and replaced with a nearly pipped clutch, which has been incubated artificially. The object is to shorten the wild hen's setting period, and thus reduce the risk of loss. This is known as the "Euston System." It is often used for Hungarian partridge in Europe.

Excess eggs may be artificially incubated under foster-mothers (usually domestic hens) or in mechanical incubators supplied with artificial heat. The principal risk in foster-mothers is transmission of poultry diseases to the chicks, and breaking of eggs or trampling of chicks by the foster-mother.

Chicks resulting from artificial incubation may be brooded and reared (1) by the foster-mother; (2) in mechanical or feather brooders; (3) by adding them to wild broods; (4) by giving them to wing-clipped cocks for "adoption." The fourth alternative has been successfully employed only in bobwhite. (See

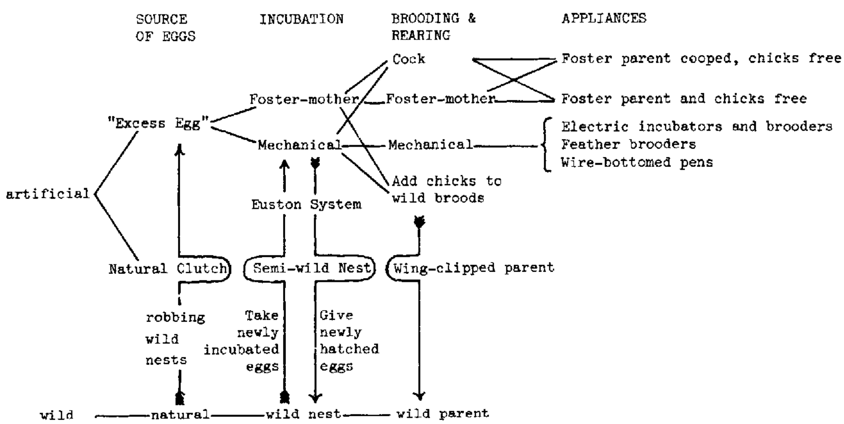
Coleman in Stoddard, 1931.) It is possible only in monogamous species where the cock normally shares in the care of the young.

Foster-mothers are usually confined in a brooder coop, from which the chicks have free egress and ingress, but foster-fathers (wing-clipped cocks) are given the free run of a pen with their chicks, or even liberated at the age of one week to raise them in the wild (Stoddard, p. 474).

New Appliances. Oil-heated incubators and oil-heated brooders for single batches of eggs or chicks have long been used with success for poultry, and with more limited success for game.

FIG. 30

BASIC TECHNIQUES FOR ARTIFICIAL PROPAGATION



More recently, electrically heated "battery" incubators, arranged to hatch a continuous series of unit batches, have come into use. Both good and bad results are reported, probably depending on whether or no the temperature and humidity schedules were adapted to the species in hand, and on how uniformly the various parts of the interior adhered to schedule. Proper schedules for poultry have been scientifically determined by agricultural research agencies. After proper schedules for the various species of game are determined, success should follow.

"Feather brooders," in which the chicks supply their own heat, are now being used successfully. These have the advantage over foster-parents of being subject to periodical disinfection.

Probably the most important recent contribution to the art of propagation is the use of wire-mesh floors, elevated above the ground, for brooding and rearing pens. Such floors automatically eliminate contacts with fecal droppings and stale food, and thus greatly decrease the disease risk. It seems probable that many difficult species, such as the grouse, will be successfully reared on wire-mesh.

Fig. 30 portrays, somewhat imperfectly, the nature of the basic techniques for artificial rearing, with their various intergradations and appliances.

Bibliography. Table 45 refers the reader to selected literature (see Bibliography) giving detailed instructions for rearing the various species. Instructions for liberating artificially reared stock are usually included with those for rearing.

TABLE 45

PUBLICATIONS ON ARTIFICIAL PROPAGATION

Species	Author	Date	Title or Description of Subject
Pheasant	Maxwell	1913	Rearing, stocking, driving, management in Britain
	Simpson	1927	"Pheasant Farming"
	Michigan	1929a	"Hatching & Rearing Pheasants" (Mich.)
	Beyer	1930	"Small and Large Scale Pheasant Breeding"
	Bartley	1931	"Pheasant Breeding Manual"
	Hiller	—	"Hatching and Rearing Ringneck Pheasants" (Pa.)
	Callenbach et al	1932	Artificial incubation and brooding
	Grimmer	1932	"Pheasant Propagation Handbook"
Bobwhite Quail	Coleman and Stoddard	1931	A complete manual, including Bantam System, Brooder System, Adoption System. (See Stoddard, Chapter 18.)
	W.Va. Wild Life, April	1930	McCarthy Back Yard Method
	Bartley	1931	"Quail Breeding Manual"
Mallard and other Waterfowl	Maxwell	1913	Brief general account (England)
	McAtee	1930	"The Propagation of Aquatic Game Birds"

TABLE 45 (Continued)

Species	Author	Date	Title or Description of Subject
Hungarian or Gray Partridge	Maxwell	1911	Euston System (p. 109), French System (p. 118)
	Page	1924	Hand rearing eggs from spoiled nests. Chapter VI. (England)
	Simpson	1927	Distinguishing sex; history in Northwest
		(1931, photo)	Criteria for telling sex
	Sprake	1930	Chipped Egg System, Chapter III.
Wild Turkey	Quarles	1918	"The Wild Turkey at Woodmont"
	Jull & Lee	1928	"Turkey Raising" (domesticated). Farmers Bulletin
	Randall (Series beginning - 1930)		Standards for wild breeding stock methods, etc.
Grouse	Committee	1911	"Grouse in Health & in Disease", Chapter XXII. Experimental rearing of red grouse by various methods in Britain.
	Job	1923	General directions pp. 55-65; Bendick System, p. 272
	Allen	1929, 1931	Last two of a series since 1925
	Malamphy	1931	"Ruffed Grouse from the Breeder's Angle"
	Luttringer	1931 b	"Raising Ruffed Grouse"
Deer	Lantz	1916	"Deer Farming in the U.S."
General	Job	1923	"Propagation of Wild Birds" (incl. aviary species)
	McAtee	1927	"The Propagation of Game Birds"
		1929a	"The Propagation of Upland Game Birds"
	Various Authors	1928-31	"Game Restoration Program" (Series of papers in "National Sportsman" and "Hunting and Fishing")
	Hopkinson	1926	Record of species bred in captivity

* For full reference see Bibliography.

NESTING STUDIES

The preceding chapters have described techniques for the measurement and control of particular factors. Some of the most important techniques, however, deal with the problem of detecting *what factors* are at work, and simultaneously measuring their joint effect on productivity. Nesting studies (including nest and juvenile mortality) are a good example.

Equivalent studies in mammals are of course equally important, but methods are less fully developed.

The precise objects and methods of nesting studies vary greatly with local circumstance. For a complete model of a nesting study the reader is referred to Stoddard (1931). I will here attempt only (1) a compilation of the nesting characters of the more important game birds, and (2) brief comments on their use in research or in practical operation of a game range.

These nesting characters are supplementary to those already discussed in Chapters II, III, IV, and XII.

The characters are treated in chronological sequence. Those which are known to vary significantly as between species are summarized in Table 46.

Dates of Nesting. There are two elements in the time-distribution of game-bird nests: (1) the date at which the earliest nestings begin; (2) the duration of re-nesting attempts, or (in the case of the few species which sometimes raise two broods) the duration of second broods.

Our grouse and pheasants usually begin nesting a little earlier in the spring than Hungarian partridges and quail in the same locality.

Maxwell (1911) says that in Hungarians, "the old birds nest a week or so earlier than the young ones." This difference has not been established as existing in this country.

Re-nestings in bobwhite may extend practically to fall frosts. Our grouse appear to be much less persistent, but pheasants may keep at it until September (Wight, 1930). In Hungarians practically all hatching is over by July 15 (Yeatter, 1932) and the same is true in England (Page, 1924, p. 33).

In extreme climates, such as Arizona, gambel quail show evidence of a double period of nesting (Gorsuch, 1932), the first in early spring when vegetative growth and insects flourish as a consequence of the winter rains, and the second (doubtless renestings) in July, when the summer rains revive the vegetation. That this double period is a phenomenon either of nutrition or cover is indicated by Gorsuch's observation that in *irrigated val-*

TABLE 46

NESTING HABITS

Species Authority	Clutch	Interval between eggs (days)	Eggs covered?	Desertion limit (days after incubation)	Incubation period (days)	Cocks may incubate?	Rest periods	May rear second brood
	1	2	3	4	5	6	7	8
BOBWHITE QUAIL								
Stoddard (1931)	(8-24) 14.4	1 or 1 +	no	?	23-½	yes	afternoon(1-7 hrs)	no
Errington (1932)	(9-19) 15.9	?	no	?		yes		no
RUFFED GROUSE								
King (unpub.)	(8-16) 12.5	usually 2	no	?	24	no	irregular	no
Schmidt (unpub.)	(6-15) 11.5	sometimes 1						
PINNATED GROUSE								
Gross (1930)	(7-17) 11.5	1.5-2.0	sometimes	?	(21-28?) 23	no	dawn & evening	no
Schmidt (unpub.)	(?) 12.7							
SHARPTAIL GROUSE					21?			
Schmidt (unpub.)	(7-14) 12.4	1.5?	no	10	24*	no	dawn & evening	no
WILD TURKEY								
Quarles (1918)		?	no?	?	28	no	weekly	no
Barrows (1912)	(10-18) 12?							
MALLARD								
Bent (1923)	(6-15) 10	?	?	?	(25-29) 26	no	?	no
Grinnell (1918)	(5-14) 10?	?	yes	?	28	no	at night	no
RINGNECK PHEASANT					22			
Maxwell	(8-15)	?	sometimes		23-24	rarely	dawn & 4pm.	?
Wight (1930)	(7-16) 11.5	?	no	14		no	dawn & 4pm.	no
HUNGARIAN PARTRIDGE								
Sprake (1930)	(9-14)	1.3	yes[x]	7	23-24	no#	irregular	?
Yeatter (1932)	(8-25) 16.4	1.4*	yes[x]	5	24	no#	morning & evening	no
Maxwell	(14-16) 15		yes[x]	2	21	no#		
Page (1924)		2 at first 1 later	yes[x]	7	23-24			
RED GROUSE								
Grouse Report	(6-17) 7	3-6*	often	?	23-24	no	morning & evening	no

Does not incubate, but helps brood young.
* In captivity.
x Always left uncovered for one day between laying of last egg and beginning of incubation. First eggs may also be left uncovered. During incubation eggs not usually covered during rest periods.

leys re-nesting continues uninterrupted. Stoddard's observations show no double period in southern bobwhites, where rainfall and vegetation continue all summer.

Clutch. Column 1, Table 46, gives in parentheses the extreme limits of variation in clutch observed by various authorities, followed by the average number of eggs comprising a clutch. Where the average shows a decimal fraction, it means that it has been computed from a considerable number of recorded nests with full complements of eggs.

The extreme maxima are, of course, often the product of more than one hen. Stoddard calls these "compound sets."

Nearly all authorities believe that the first clutches of the season are larger than those of the later re-nestings. Stoddard (p. 28), however, thinks that in bobwhite this progressive decrease is "largely due to the compound sets, which are found mainly before nesting cover becomes dense." Errington, however, believes that there is an actual progressive decrease in clutch over and above what might be ascribed to compound sets. He found:

TABLE 47

SEASONAL DECLINE IN CLUTCH, BOBWHITE, WIS.

Complete Clutches		Average Number of
Begun in	Number of Nests	Eggs in Clutch
First half of May	11	19.2
Last half of May	6	16.6
First half of June	9	17.0
Last half of June	6	14.2
First half of July	5	13.8
Last half of July	3	11.3
August	2	9.0

There are also indications of a difference in average clutch as between years. An alleged instance in spruce partridge, not supported by adequate figures, has already been mentioned in Chapter IV. Yeatter (1932) found the Hungarian clutch in Michigan averaged 17.4 in 1930 and 16.1 in 1931.

The *Grouse Report* (p. 8) quotes, and apparently accepts, Seeholm's statement that in red grouse:

". . . the number of eggs laid would seem to vary with the propitiousness or otherwise of the season. In very wet and cold springs, 4–9;

in very favorable season, 6–12. In an average year most nests will contain 7–8 eggs. Birds which breed late on the high grounds do not seem to lay fewer eggs than those which breed early in the more sheltered situations."

Interval Between Eggs. The probable clutch is of value to the observer of nests because it enables him to guess, when a nest is found, whether or not the clutch is complete. If incomplete, he must guess how soon it will be completed, because his subsequent visits will be timed accordingly. For this, he needs to know the usual time interval between eggs characteristic of the various species. Column 2, Table 46, gives this interval in days in so far as it is known.

Stoddard says of bobwhite:

"Normally an egg is deposited each day until the set is complete, or progressively at a later hour each day till laying time comes late in the evening, when (that) day is skipped and laying is resumed at an early hour next morning."

Apparently an egg a day is the fastest laying rate of game birds, and even bobwhite does not always attain it. The interval seems to increase with the size of the species.

The interval is not always uniform. Gross (1930*b*) says that in pinnated grouse, while the interval averages two days or less, "certain eggs of the set are laid on successive days, to be followed by a lapse of two or more days before the next egg is deposited." These lapses, he thinks, "probably depend on . . . the weather, the state of health of the bird, and the available food."

Page implies that in Hungarian partridge the rate speeds up as the set nears completion: an egg is deposited daily after the seventh or eighth egg, but not before.

An extraordinarily long maximum interval is indicated for red grouse. The *Grouse Report* (p. 8) says:

"The intervals between the laying of each egg vary enormously in captivity, probably also in nature, depending upon the weather; for example . . . one hen took 29 days to lay 10 eggs . . . another laid only 4 eggs in 26 days."

Covering of Eggs. A character of outstanding importance in the always difficult job of nest hunting, and of diagnostic value after the nest is found, is the habit, characteristic of some species, of covering the eggs with feathers or nesting material. The nest hunter must know whether to "set his eye" to look for eggs or for egg-covers,—two very different matters. Having found a nest, he can in some species tell its stage of advancement by the presence or absence of covering.

The only species which never cover their eggs are bobwhite, pheasant, ruffed grouse, and turkey. Wight has found a little covering on a few pheasant nests, but it was apparently accidental. Maxwell, however, says pheasants sometimes cover their eggs in England.

Pinnated grouse sometimes cover their eggs, and red grouse often.

Mallards and Hungarians regularly cover their eggs, except that Hungarians, Sprake says, do not usually cover the first egg, nor is any covering used when the hen is absent from the nest for "rest periods" during incubation. Moreover all authorities on Hungarians agree that the eggs are left uncovered between the laying of the last egg and the beginning of incubation. An uncovered Hungarian clutch, therefore, is diagnostic of incubation, either under way or about to begin, whereas a covered nest is diagnostic of incompleteness.

The egg-covering used by waterfowl is always breast down. That used by gallinaceous birds is always vegetation. Incubating mallards sometimes cover themselves with vegetation while incubating.

Roofing, Orientation, and Location. Covering placed over the eggs, and the arching vegetation sometimes roofing the nest, are of course two different things. Knowing whether nests are roofed, and if so in what direction the opening or "tunnel" faces, helps in locating them. Stoddard found 64 per cent of bobwhite nests roofed. Seventy-four per cent were located within 50 feet of some open spot, and in most of these the "tunnel" faced or paralleled such opening. Nests were as likely to face toward one point of the compass as another, but seldom faced down hill. Nearly 90 per cent were in dead growths of the previous season.

Errington found 80 per cent of quail nests either roofed or under the equivalent of roofing. His findings as to location agree with Stoddard's except that he saw no tendency to avoid downhill facing. He could see no plain tendency to locate nests in sun or shade. Bluegrass of the preceding year's growth was the favorite nesting cover.

The growths selected as nesting cover have already been discussed in Chapter XII.

Dropped Eggs. Single eggs are sometimes dropped at random by all game birds. In bobwhite, Stoddard (p. 28) considers such eggs as an indication of recent nest destruction, the egg being dropped before re-nesting can begin. Occasionally, he thinks, they indicate that some hen was forced to lay before she could reach her nest. Blue geese are said to drop eggs even before setting out on their spring migration (McIlhenny, 1932, p. 294).

Incubation Interval. Most gallinaceous birds normally begin incubating within a day or two after the completion of the clutch, but Stoddard (p. 29) has seen delays up to a week in bobwhite, while Sprake reports intervals of nearly a week in Hungarians.

Desertion. Nests are deserted upon slight provocation before laying has begun and while the clutch is incomplete, but the hen becomes more and more tenacious as incubation advances. Hungarians, according to Sprake, will occasionally return even to nests cut over by a hay mower, provided the eggs be within a day or two of hatching. Yeatter says that of 15 incubating Hungarian hens surviving after the mowing-over of 18 nests, 6 returned to the job, and 5 brought off a brood. Errington found that quail returned to 2 out of 18 mowed-over nests. Wight found pheasant nests mowed over within two days of hatching were reoccupied. Until backed by more figures, however, such tenacity must be considered exceptional in all species.

The practical question is: At what point can the observer safely count on the hen's return after and in spite of an ordinary disturbance, such as flushing her off the nest, or handling her eggs? Of the authorities cited in Column 4, Table 46, only one thinks there is much risk of desertion from mild disturbance in any species after seven days of incubation. This may be called the "desertion limit." It is a very important character to know in detailed research work, or in operating the Euston system or chipped egg system.

Incubation Period; Participation of Sexes. The ordinary limits of variation in incubation period, plus an average where known, are given in Column 5, Table 46 (also in Table 1*a*). Column 6 tells whether one or both sexes may incubate.

The length of the incubation period appears to vary with the "heat" of the bird and the weather. An exhaustive treatment of incubation phenomena is that by Bergtold (1917). Incubation behavior in bobwhite is described in detail by Stoddard (pp. 29–36).

Maxwell (1911) also alleges that "the eggs of birds (partridges) imported from Hungary often take longer to hatch than those of the native birds." It is an open question whether this difference, if it exists at all, is the result of transporting the eggs, or a true difference between geographic races.

Bobwhite seems to be the only gallinaceous bird in which the male may commonly incubate, although the Hungarian cock shares in the care of the young.

Incubated nests can often be distinguished by the arrangement of the eggs, which line the nest cup in a single layer, whereas previous to incubation they are likely to be piled irregularly.

Dead eggs may be incubated by quail up to 56 days (Stoddard, p. 35), and dummy eggs by Hungarians up to 30 days (Sprake).

Yeatter found two Hungarian hens incubating full clutches of dead eggs, at least one of which had persisted beyond the normal hatching time. Just when and by what token hens desist from incubating dead clutches is still unknown. There is a widespread popular belief that they persist indefinitely—some say until the eggs are "blackened and polished." There is as yet no solid basis for such reports.

Bobwhites were found by Stoddard (p. 39) to hatch on the average around 85 per cent of their eggs, but 38 per cent of the nests hatched every egg. Five per cent of the total eggs were infertile, and the same per cent contained dead embryos presumably due to chilling after disturbance of the hen. The bulk of the unhatched eggs occurred in a small portion of the total nests.

The extraordinary effects of drouth on hatching are discussed by Stoddard (p. 39) and Leopold and Ball (1931). The effect of frost and cold are discussed by the *Grouse Report*, pp. 9–13.

Rest Periods. Incubating game birds of most species leave the nest for rest and food so frequently and for so long as to suggest that oscillating temperatures are optimum for incubation. Column 7 indicates that two rest periods per day, in the early morning and late evening respectively, are the rule, but there are three exceptions. In bobwhite one long afternoon rest period prevails (Stoddard). Turkeys leave their nests only about four times during the whole incubation, or once a week (Quarles, 1918). Mallards leave the nest only at night (Grinnell *et al.*, 1918).

Chipping Period. It is difficult to separate the period of actual chipping or pipping from the subsequent period of brooding and drying which precedes permanent departure from the nest. All observers of the sum of the two periods agree, however, that it is between 24 and 48 hours. Schmidt had one sharptail nest which appears to have completed chipping and been eaten by some predator between observations 14 hours apart. To know the length of this period is of great importance in operating the Euston system, and in research studies.

Game birds rarely return to the nest once the brood has been led away, but three returns by Hungarian broods are reported by Sprake, all, however, during wet weather and to a nest site offering better shelter than the surrounding terrain.

Feigning. Another character of great importance in making a census of broods is that of feigning. The parent, on the approach of an intruder, feigns to be crippled and thus advertises the presence of the brood. All game birds feign more or less when with chicks, and some even when disturbed during late incubation, but the practical utility of the character for census purposes depends on whether such behavior can be *counted on*, and if so, up to what maximum distance, and during what age interval of the chicks? This question cannot yet be answered. A method of brood census for ruffed grouse, based on feigning, is described in Chapter VI, on "Game Census."

Use of Nesting Characters. The foregoing characters of the various species represent either:

1. Normal behavior, against which abnormal conditions can be measured, or
2. Diagnostic characters, by which the status of observed nests or broods may be inferred.

On these characters the observer may build his own methods of observation for research studies of nesting habits and losses, or his own methods for the diagnosis and control of nest mortality on managed areas.

The first requisite for either project is to find and mark the locations of a large number of "going" nests. Nest-finding is the *bête noir* of many a game bird student. Few people who have, by accident, stumbled upon one nest realize how hard it is to go out deliberately and find a large number. Large numbers are necessary for sound conclusions on nest mortality.

Offering cash rewards for occupied nests, or otherwise making sure of the co-operation of local residents, usually brings in many more nests than personal search. Early nests, when vegetation is short, are easier to find than late ones after vegetation becomes heavy. Mechanical methods for finding hayfield nests are described in Chapter XII. These are the only suggestions for nest finding which apply to all species and all terrain.

The technique developed by Stoddard and described in *Bobwhite* (p. 187) is the pattern for nest studies, and will remain so for years to come. It consists essentially of daily or frequent visits to a large series of going nests to determine the habits of the bird, or, if the observer finds the nest has been destroyed, to determine the identity of the destroyer. Weather, agricultural machinery, and predators, are the three causes of desertion or destruction. The first two are discussed in Chapter XIV, and predators in Chapter X. Desertion has been discussed in a previous caption.

The *ex post facto* identification of the predator which has robbed a nest is one of the real tests of a game manager's skill. The rate and manner of taking the eggs, the shape and disposition of the eggshells, tracks or hair left on the spot, whether and how the incubating bird was killed, and other criteria are described by Stoddard, and can be used by others if they learn how.

Nest Mortality. The total nest mortality in a representative series of wild nests on unmanaged terrain is seldom less than 50 per cent, and may run much higher. Table 48 indicates that the average loss for all species as measured by nesting studies to date in this country, is 61 per cent, a figure eloquent of opportunity for the game manager.

It is significant that in all the wealth of nest protection technique described by European authors, I can find no single instance of a systematic series of counts of nest mortality in the managed areas which they describe. One may infer, however, that it is lower than in the counts described in Table 48. Page

TABLE 48

NEST MORTALITY

Species Locality, Years	No. of Nests	No. Lost or Deserted	Number Hatched	Authority
BOBWHITE				
Georgia, 1924-27	602	385	217	Stoddard, p. 184
Wisconsin, 1929-31	68	34	34	Errington, unpubl.
RUFFED GROUSE				
Minnesota, 1929-31	12	1	11	King, Unpubl.
New York, 1930	14	9	5	Bump, 1930
Wisconsin, 1931	4	2	2	Schmidt, unpubl.
PINNATED GROUSE				
Wisconsin, 1929-30	40	20	20	Gross, 1930
Wisconsin, 1931	15	6	9	Schmidt, unpubl.
RINGNECK PHEASANT				
Michigan, 1928-30	50	33	17	Wight, 1930
HUNGARIAN PARTRIDGE				
Michigan, 1929-31	74	48	26	Yeatter, 1932
GAMBEL QUAIL				
Arizona, 1931	22	15	7	Gorsuch, 1931
SHARPTAIL GROUSE				
Wisconsin, 1931	19	8	11	Schmidt, unpubl.
SCALED QUAIL				
Arizona, 1931	10	8	2	Gorsuch, unpubl.
Total	930	569	361	
Per Cent	100	61	39	

(1924, p. 89), in England, evidently made a rough count on which to base his general statement: "Whatever care is taken, the preserver (of Hungarians) who loses from any cause less than 5 per cent of his nests is fortunate." Yes, indeed!

Juvenile Mortality. As already pointed out in Chapter VII, the measurement of juvenile mortality is the most difficult feat in game management. It must usually be accomplished by "subtraction," *i. e.*, by measuring the other factors, and the fall crop, and ascribing the difference to juvenile mortality.

Wight (1930) made a partial measurement of juvenile mortality in Michigan pheasants. He found a 3.5 per cent shrinkage between "the time of first observations to the time of (fall) dispersal." This figure probably represents an exceptionally favorable outcome.

Yeatter (1932) obtained, by subtraction, an estimated juvenile mortality equal to 20 per cent of the whole population in Michigan Hungarians.

Errington (1932*a*) estimates a 25 per cent mortality in Wisconsin quail, between the time of hatching and September.

In the study of juvenile mortality, food habits, and brood behavior, the game manager is often confronted by the necessity of estimating the age of chicks or young birds killed by predators, found dead of disease, or taken as specimens. Comparison with a series of juvenile skins is the most accurate way to judge age in chicks, but when skins are not available, the weight is a good index. Fig. 31 gives the juvenile weights determined by Stoddard (p. 72) for bobwhite, Wight (unpublished) for pheasant, Yeatter (unpublished) for Hungarian partridge chicks, and Gross (1930*b*) and Schmidt for pinnated grouse. A description of juvenile plumages and weights in pheasant is also given by Leffingwell (1928, p. 18).

TRAPPING GAME

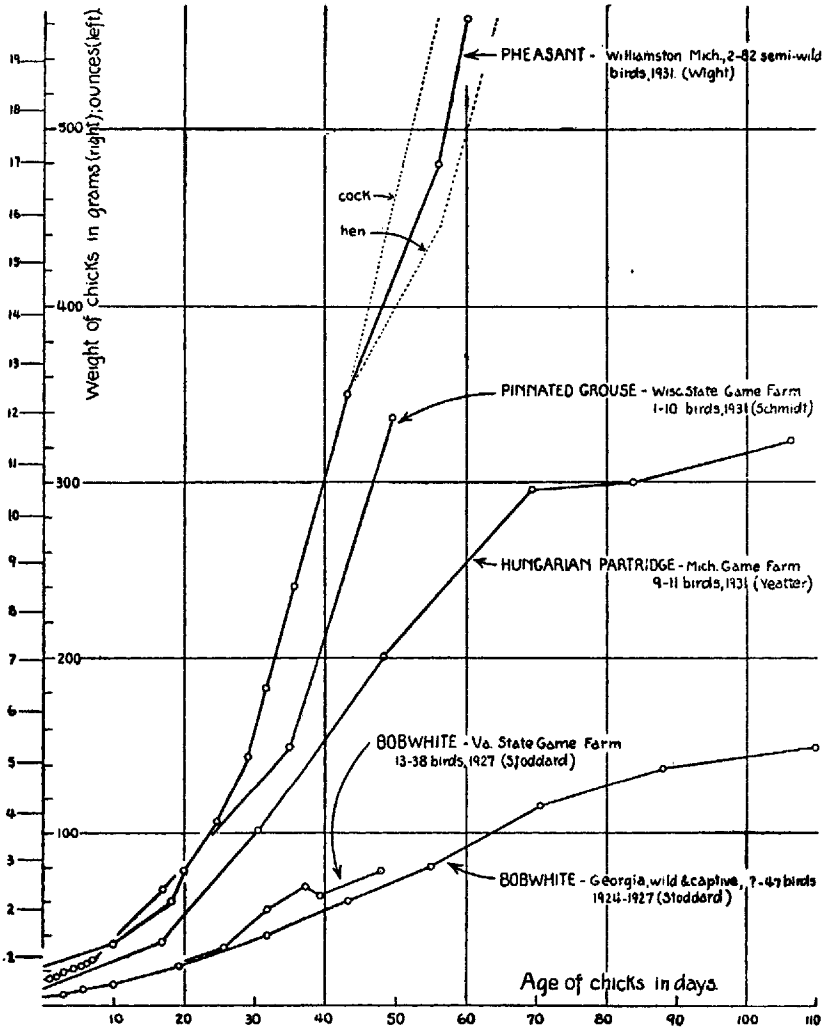
Banding studies such as those referred to in Chapter VI, the artificial extension of outflow from refuges described in Chapter VIII, and the capture of initial stock for artificial propagation, all demand the trapping of wild game, alive and without injury, and often in large numbers.

Most live-traps depend on a display of bait. The bait is usually some preferred food, but sometimes a live female is the most effective (Stoddard, p. 446).

Corrals or nets are often successful, without bait. Grinnell (1925) and Austin (1930, unpublished) have pointed out the undeveloped possibilities of nets as tools for ornithology in this country.

FIG. 31

WEIGHT: AGE CURVE OF CHICKS



In special cases game may be captured cheaply and easily by "shining." Shining of pheasants is referred to in Chapter IV.

The game manager who has need of live-trapping technique should follow down the leads suggested in Table 49. A bibliography on trapping techniques for predators has already been given in Chapter X.

TABLE 49

LIVE-TRAPPING TECHNIQUE

Species	Device	Authority, Locality, Remarks
Deer & Antelope	Salted corrals with trip & trigger gates	Birmingham (1931), New Mexico, Not successful for deer
Deer	Corral with trip gate on waterhole	Locke (1929), Arizona
Mountain Sheep	Salted corral with self-trip gate	Round (1928), British Columbia
Bobwhite	Traps and nets	Stoddard (1931, p. 439), Georgia
Hungarian Partridge	Baited trap. Type ?	W. B. Grange, Fish Creek, Wis.
Ducks and Geese	5 types of trap	Lincoln & Baldwin (1929, p. 65)
Birds in general	For banding, many types	Bird Banders Manual, Lincoln & Baldwin (1929), also Baldwin (1931)
Geese	Trip gate pen	Miner (1923, pp. 142-146), Ontario
	"Waterlily"	Austin (1932a)
Authorities Who Have Not Published		
Scaled Quail		J. S. Ligon, Carlsbad, New Mexico Paul Russell, University of New Mexico
Gambel Quail	Box	David M. Gorsuch, University of Arizona
Ruffed Grouse	Many devices	R. T. King, University of Minnesota
Prairie Chicken & Sharptail	Traps	F. J. Schmidt, Wis. Conservation Commission
Pheasants	Shining	Oscar Johnson, State Game Warden, South Dakota
Birds	Clapnets	Wm. I. Lyons, Waukegan, Ill.
Diving Ducks	Baited trap	O. L. Austin, Jr., N. Eastham, Cape Cod

GAME MAPS AND RANGE TALLIES

A penetrating observer of human foibles (Briggs, 1931) has aptly said:

> "To make a map is a courageous thing to do. No one but an artist, an egotist, or a topographical engineer would try it without grave provocation. *Equivocation is impossible.* Maybe all (natural) historians ought to make maps."

The italics are mine, also the parenthetic insert. To him who has searched the largely mapless early literature of game for usable facts, neither the quotation nor the liberties I have taken with it will need comment.

Purposes. Facts concerning game distribution, behavior, history, and management can often be accumulated on maps or tables to better advantage than in notes. Provided the symbols and format be adequate, maps and tables are easier visualized, analyzed, and reproduced than notes. A frequent predicament of field workers is to accumulate so many notes that time is lacking to analyze them, or to have notes string out over such a long period that the earlier ones are lost or hard to segregate by the time a sufficient volume are at hand to warrant a conclusion. Cumulative maps and tables are the answer to both difficulties.

To make the most of his powers, every game manager should be skilled in the use of these mechanical aids. A working knowledge of the theory of statistics, and of the theory of probabilities, will help him make accurate deductions from his data.

Only a few samples of the infinite variety of possible graphic game records can be here included.

Base Maps. Any venture in game mapping should begin by getting the best possible base map. Only in the wilderness will the game manager have to draw his own base. In any region covered by General Land Office surveys, a tracing of the original township plat can be made, or a plain blank township outline used. Where the U. S. Geological Survey has made topographic maps, copies can be purchased for a few cents, and photographic enlargements made of the spot to be covered. In farming country, the county usually sells "Plat Books" showing by townships all the farm boundaries, streams, roads, etc. These are invaluable. Many states and federal bureaus issue accurate detailed maps of lakes and navigable rivers and coastlines. Some agricultural colleges provide their field workers with complete sets of county outline maps for the state.

Where no base is available, or where an accurate very detailed base is needed for a large area, an aerial photographer may be employed. Aerial maps are coming into widespread use for many purposes. The cost is high, especially for small jobs, but their wealth of detail makes them especially valuable for game work. A small section of an aerial map is shown in Stoddard's Plate 34, p. 172.

Mapping Methods. Most jobs of game mapping call for entering types, census figures, banding returns, or similar data on a pre-existing base. Sometimes areas must be measured. In either event it is a matter of mapping the location of certain spots or lines on the base. For this purpose, the method employed by timber cruisers is quick and sufficiently accurate: Go to some point on the ground which is clearly located on the base map (such as a section corner, a highway intersection or a farm house). Pace north, south, east, or west toward the things to be mapped, keeping direction either by compass or by paralleling fencelines. Every eighth of a mile (120 double paces) stop, scale off the distance on the map, and sketch in the objects nearby which are pertinent. Close in at some other known point, or return to the point of beginning after pacing a circuit or traverse of the country to be mapped. Fig. 33 was thus drawn, using a hand-made enlargement from the County Plat Book as a base, in half a day.

Type Maps. Most game research projects centred in a limited locality, and all management projects dealing with limited acreage or land purchase, demand a basic type map of the area to be covered. Such a type map can be made either by "cruising" or by aerial photography. The boundaries of types can be easily seen on a good aerial map, and their areas planimetered, as on any other map.

Fig. 32 shows a simple type map of a 1500-acre tract in southern Wisconsin. The base was obtained from the County Plat Book. The detail was added by cruising, and required two days' field work. A separate legend shows the food and cover improvements installed for pheasants and quail by the farmers on the area, cooperating with a group of sportsmen.

A more elaborate classification of types, mapped on a larger

Fig. 32

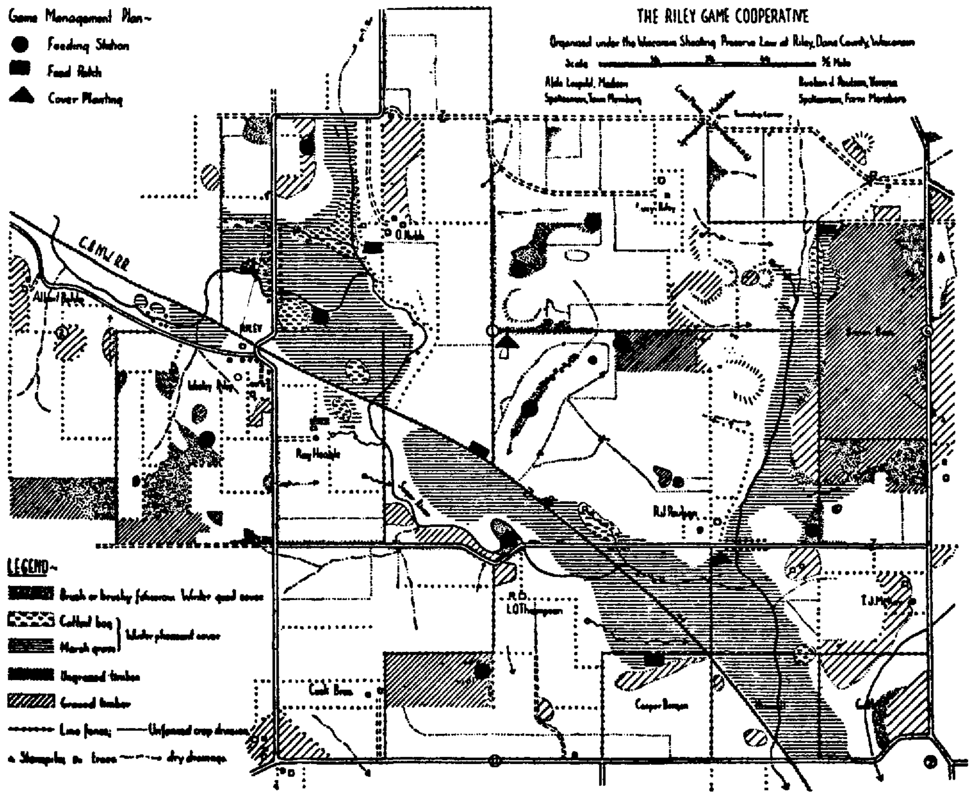

THE RILEY GAME COOPERATIVE
Organized under the Wisconsin Shooting Preserve Law at Riley, Dane County, Wisconsin
Scale
Aldo Leopold, Madison
Spokesman, Town Members
Spokesman, Farm Members
Game Management Plan ~
Feeding Station
Food Patch
Cover Planting
LEGEND ~
Brush or brushy fencerow. Winter quail cover
Cattail bog
Marsh grass
Winter pheasant cover
Ungrazed timber
Grazed timber
Line fences; Unfenced crop drainage
Slough or trees
dry drainage
C.M.&N.RR
RILEY
Ray Haight
L.O. Thompson
Cook Bros.
Cooper Brown
T.J. Miller

TABLE 50

RANGE COMPOSITION TALLY

Type		Kewanee, Ill.- Burlington, Ia.		Ft. Madison, Ia.- Marceline, Mo.	
		No. Tallies	Per Cent	No. Tallies	Per Cent
Food:	Shocked Corn	0	0	3	1
	Standing Corn	41	30	33	13
	Stubble	25	18	55	21
	Reverted Fields	0	0	7	2
	Orchard	1	1	2	1
Cover:	Ungrazed Woodlot	2	1	16	6
Both:	Heavy Weeds, Brush, Grass	3	2	7	3
Neither:	Pasture	24	17	87	33
	Plowed (incl. winter wheat)	24	17	18	7
	Grazed	6	4	25	10
	Towns	14	0	8	3
		140	100	261	100

area by cruising, is that prepared by K. C. McMurry of the Department of Geography, University of Michigan, for the Izaak Walton League, covering Williamston Township, Ingham County, Michigan. The plan of management built up on the basis of this map is described by Wight (1931). The Williamston map is not here reproduced because reduction to book-size would make it illegible.

Composition Tallies. The game manager must frequently compare the value or appraise the condition of blocks of game range so large that cruising is impracticable, or so nearly alike that mental impressions alone do not suffice to show which range is the better, or what is the precise condition of either. In this event some systematic method of tallying samples can be employed to advantage. No map is required.

For example: The per cent composition of a large block of country can be easily obtained, without a map, by tallying the types at fixed intervals while riding across it in a car or train. Table 50 summarizes a range composition tally taken every 30 seconds from a fast train in the prairie and riverbreaks type of Illinois and Missouri in March, 1931. The figures in the first and third columns represent the sums of the tally marks on the original tally sheet.

Each tally mark represented the type of food or cover occurring just outside the right-of-way fence at the time the watch (held in the hand) passed the 30-second mark.

Such a method, of course, shows only the comparative *frequency* of each type, not its actual position, nor the degree of interspersion. Aerial photographs are an ideal way to measure composition, position, and range interspersion simultaneously, but cost a good deal of money, whereas such a table as this costs nothing over and above travel mileage.

Habitability Tallies. The proportion of any large range which offers habitable combinations of visible factors, such as food and cover, can be measured by means of a tally made at fixed intervals from a motor or train, provided:

1. The time of year is that of the critical season.
2. The range is open enough to see and identify the food and cover types for at least one cruising radius from each point of observation, or station.
3. The species in question is a coveying bird which occurs, when it occurs at all, in population units of practically fixed size.

These criteria are satisfied in the case of winter quail range, but they hardly admit any long-radius game, nor forest game, nor farm game like pheasants. A given spot might winter anything from one to several hundred pheasants and accordingly there would be no sharp line between habitability and non-habitability on which to base a tally. On the other hand a given spot either has, or has not, the food and cover necessary to hold a covey of quail.

It is barely possible that Hungarian range might be tallied for per cent habitability.

Table 51 is the combined result of five habitability tallies for five blocks or sections of quail range made from a train in March, 1931. Table 52 compares the five blocks. The separate tallies for each block are omitted to save space,—they are similar to Table 50.

TABLE 51

HABITABILITY OF QUAIL RANGE AND COMBINATIONS OF FOOD AND COVER IN PRAIRIE AND RIVERBREAKS TYPES

From tally of 789 samples in N.W. Illinois, N. Missouri, S.E. Iowa & E. Kansas.

Figures without circles: per cent of total samples habitable.
Figures in circles: per cent of total samples not habitable.
"T" means Trace (less than one per cent).

Aldo Leopold
March, 1931

		Usually Food Bearing (45 per cent)										Usually Foodless (55 per cent)										Total	
		Shocked Corn		Standing Corn		Weeds		Weedy Stubble		Feedlots		Winter Wheat		Weedless Stubble		Pasture		Plowed		Towns			
		H	N-H	H	N-H	H	N-H	H	N-H	H	N-H	H	N-H	H	N-H	H	N-H	H	N-H	H	N-H	H	N-H
Usually sufficient cover (27 per cent)	Ungrazed Woods or Brush			3		1		T				1		1		1	(1)					6	(1)
	Thick Hedge	T		2		T		T			(T)	T	(T)		(1)	T	(T)	T				3	(1)
	Cover Draw	T		6		2	(T)	1		T		2	(T)	T	(1)	1	(1)	T	(T)			12	(2)
	Heavy Grass or Weeds			2	(T)							T				T	(T)	T				3	(T)
	Grazed Woods		(1)	4	(T)	1		T		1	(1)	T	(T)	1	(T)	1	(4)	T	(1)			7	(7)
Usually deficient cover (7[illegible] per cent)	Thin Hedge		(T)	1	(5)	T			(1)		(T)		(1)		(2)	T	(3)		(2)			1	(14)
	Fencerow			1	(1)	T			(T)				(T)		(1)		(T)		(T)			1	(3)
	Shelterbelt			T															(T)			T	(T)
	Bare Draw				(2)		(1)		(T)		(T)		(1)		(1)		(7)		(2)		(T)		(14)
	None		(T)		(5)		(1)		(1)		(1)		(2)		(4)		(5)		(4)		(3)		(26)
	Total	T	(1)	17	(14)	4	(2)	2	(2)	1	(2)	3	(5)	1	(9)	3	(21)	1	(8)		(3)	33	(67)

Each tally mark represents an ocular appraisal of the food and cover combination obtaining within a one-fourth-mile radius immediately outside the right-of-way. Tallies were made at intervals of 30 seconds, *i. e.*, at "stations" about one-third mile apart.

The vertical columns of the tally sheet (Table 51) are the food types prevailing on the area in question, arranged in descending order of food value. The horizontal columns are cover types, likewise in descending order. The *position* of each tally mark thus represents the combination of food and cover obtaining at that station. The ultimate number of tally marks in each square is the *frequency* of that combination.

Combinations judged to be habitable were made in black (uncircled totals). Combinations judged to be not habitable were

TABLE 52

HABITABILITY BY ROUTES

Routes	No. Stations	Per Cent		Why Non-Habitable	
		Habitable	Non-Habitable	Food: Winter Wheat or Poorer	Cover: Grazed Woods or Poorer
(1) Ottawa, Kansas - Kansas City, Mo.	125	38%	62%	72%	68%
(2) Kansas City, Mo. - Marceline, Mo.	160	35%	65%	59%	72%
(3) Marceline, Mo. - Ft. Madison, Iowa	260	34%	66%	56%	74%
(4) Ft. Madison, Iowa - Chillicothe, Ill.	262	29%	71%	41%	72%
(5) Kewanee, Ill. - Burlington, Ia.	151	(?)	(?)	62%	(?)
AVERAGE		33%	67%	55%	72%

made in red (circled totals). The ultimate distribution of the colors thus indicates not only the percentage of habitable stations, but also the reasons why habitable or non-habitable.

The net conclusion of the tally was: Only a third of the total of 789 samples are habitable for quail. The constituent blocks vary from 29 to 38 per cent habitable. Food was deficient at 55 per cent of the stations, the percentage varying from 41 to 72 in the five constituent blocks. Cover was deficient at 72 per cent of the stations, the percentage varying from 68–74 in the five blocks.

When in doubt, the station was tallied as habitable. Undoubtedly the above conclusions are more optimistic than they would be if each station had been worked on foot with a bird dog for the purpose of finding actual coveys.

Cover Shrinkage Tallies. In appraising a very large and very homogeneous block of game range, decisively lacking in some visible factor such as cover, it is unnecessary to make complicated tallies of cover and food combinations or range composition. In the game survey of Iowa, for instance, it was evident at the outset that almost the whole state had an excess of food and a shortage of cover. The question was: how do the counties compare as to the frequency of cover remnants? At what rate are the remnants disappearing?

The first question was answered by a simple tally of each unit of winter cover lying within one-eighth mile of each highway travelled. The unit was "that quality and quantity of cover necessary to winter a covey of quail."

The second question was answered by making a separate tally of the vestiges or remnants of coverts which had recently disappeared, and comparing it with the tally of those which persist.

The details of both tallies, and maps expressing the compiled results, are given in the *Iowa Game Survey*.

Range Development Maps. The basic simplicity of cover and food manipulations is seldom clear to the layman when described in words. When graphically presented on a map, however, the whole principle is frequently grasped by the lay mind with all the sudden intensity of a revelation.

Moreover specific written plans for the development of a particular range are well-nigh impossible. A range development map is much the shortest and most concise way of recording recommendations. Particular spots which must be discussed in writing may be identified by key numbers or letters on the map.

Developments of cover and food are best indicated by colored symbols superimposed on a type map such as Fig. 32. Where the necessity for numerous copies precludes color, uncolored symbols may be used. Fig. 33, for example, is an inked field sketch of a typical Iowa farm reproduced from the *Iowa Handbook* (1932). The stippled spots are the cover and food developments recommended. The *Handbook* explains the proposed developments and their probable effects as follows:

PRESENT COVEYS

"*Covey No. 1* makes its headquarters in an abandoned road cut at the northeast corner of the farm (see solid circle with the figure '1' in its centre). The old road is flanked by an osage hedge. Its thorny branches overhang the steep south-facing bank, the top of which bears a 'whisker' of bluegrass and sweet clover. Such a place is wind-proof and hawk-proof. It offers dry dusting spots even in wet weather, and sunny loafing ground for winter days.

"In the 'triangle' of the road (marked 1*a*) is grass which the road crew should be asked to leave unmowed and unburned for nesting. To the south is a pasture slope bearing ragweed. Such a combination is irresistible. There will be quail here as long as there are any in the country.

"*Covey No. 2* makes its headquarters in the ungrazed woodlot near the southwest corner of the farm, adjacent to a feedlot where hogs are being fattened. The food supply is further strengthened by a cornfield to the west. The woodlot offers plenty of brush but no grass. This range is weak on grass, and hence might not be occupied in years of short quail crop. Grass should be provided by concentrating next winter's cordwood cuttings on the south slope marked 2*a*. Leave the brushpiles unburned and let grass, brambles, and oak sprouts come in. Keep the cattle out.

"These two present coveys total 30 birds on 170 acres, or a bird per 6 acres. This is a thin stand. Let us build it up into a thick one.

Prospective Coveys

"Go back to the centre of the north side of the farm. In and near the dashed circle marked '3' we can build a range for

"*Covey No. 3*. The corn to the north offers food, but there is now no grass whatever, and no brush save the grazed-out remnant of a hedge. At the corner of the clover field marked 3*a* are a few wild plums pruned up by cattle, and also a group of big limby cottonwoods. Fell one of the cottonwoods, and let it lie unlopped. Fence off the stippled area marked 3*a* so the grass and clover can grow tall, and the plums can spread be root-suckers. In the pasture at 3*b* is another corner, already partly isolated by the creek channel. Fence it, and fell a couple of the large scraggly willows on the creek bank. Let them lie with the grass growing up through the unlopped tops.

"3*a* and 3*b* together will have a new covey next fall or the fall after. Two small coverts, by the way, are often more effective than one big one.

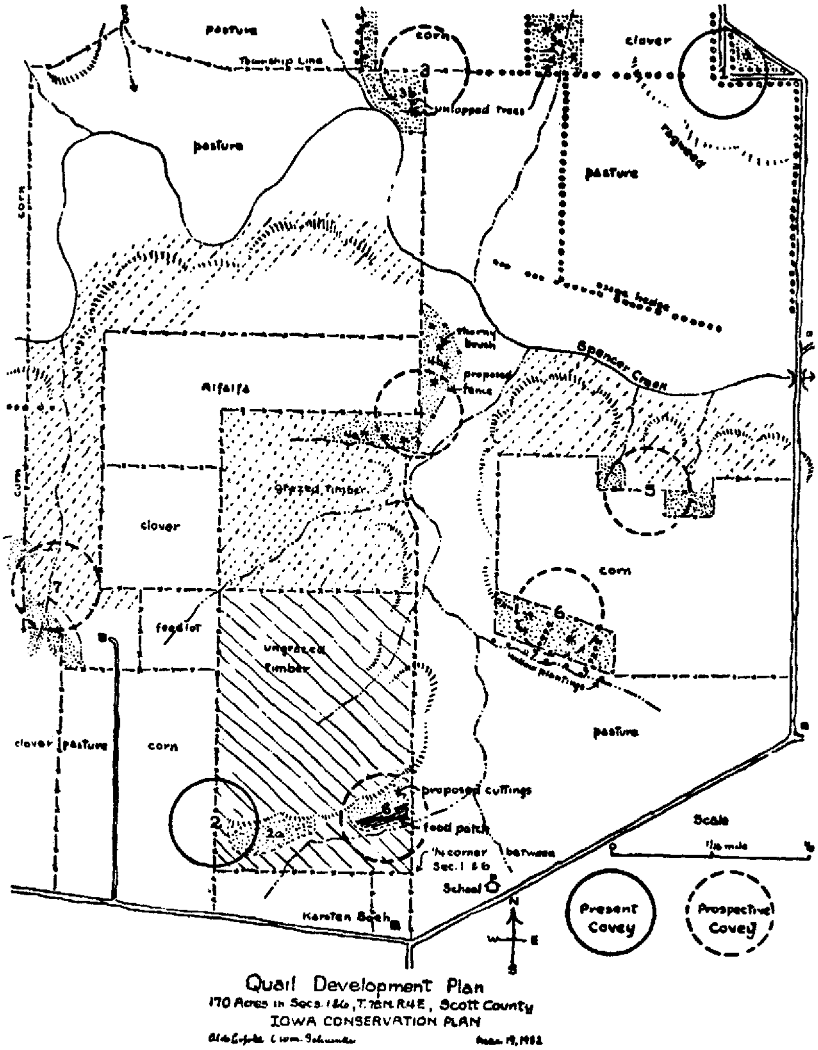
"Proceeding southward, we have a series of steep north-facng timbered banks along the south side of Spencer Creek, which are iof sligh value for pasture. They are of slight winter value for quail, too, because of their north exposure and the distance from corn. They will serve as nesting ground only. An occasional unlopped treetop, in which long bluegrass can grow, will enhance their value for this purpose.

"*Covey No. 4*. A new winter headquarters can be built up in the woodlot at 4*a* by cutting cordwood on the south-facing bank of a side-draw. There are a few haw trees in the present undergrowth. Preserve these carefully; when the sun has been let in they will wax strong and thorny. 4*a* will have to be fenced, because unlike 2*a*, this woodlot is grazed. Let the grass grow, and leave the brushpiles unburned.

"At 4*b* is a hogback in a pasture already bearing some haws, osage seedlings, and clumps of hazel and buckbrush. Fencing this to let the grass grow up will make a perfect nesting ground. In winter this patch will also catch the early morning sun on its east-facing bank, and thus supplement 4*a* as winter quarters.

"Range No. 4 is weak in that the prospective covey will have to *fly* southwest across a pastured draw to reach corn. A line of grazing-

FIG. 33



resistant osage or of brushpiles strung across this pastured draw is needed to serve as a 'street' to let the covey *walk* to the corn.

"*Covey No. 5* can be headquartered to the east of No. 4 in two fence corners at the heads of side-draws where their forks offer south exposures. These fence corners are at present pastured bare. Fencing will bring in long bluegrass, and in time, brush. Corn lies just to the south of the fence. It will help make this range habitable the first year after fencing if some temporary cover, in the form of unlopped treetops or brushpiles, is provided.

"The weak point of this range is its general north exposure. Only the south-facing sides of the east-and-west side draws at the edge of the upland are usable in winter.

"*Covey No. 6* is to be headquartered just southwest of No. 5 in a small pasture lying on a steep south slope, now ruined by erosion. This pasture now offers neither grass nor brush cover, but it is already fenced, and both grass and brush will grow up when grazing ceases. Its larger gullies are to be planted with willow cuttings. 'Pollard' these willows, and when the new growth is cut back each spring, throw the clippings into the gully to stop wash.

"There are a few haws or thornapples already started in this pasture. A few osage cuttings planted on the hogbacks would hasten the restoration of brush.

"Range No. 6 will hardly make a covey the first year, but it ought to be a 'sure bet' by the second or third year of protection from grazing. No pasture will be lost, because the present washing and gullying has left the soil too poor to have pasture value. This steep impoverished slope, on being protected, will likely come up to brome grass rather than bluegrass, but this is equally good for quail.

"*Covey No. 7* is to be headquartered on the west side of the farm where several steep eroding gullies are eating back into a cornfield. Fencing a corner of the adjacent grazed woodlot will provide additional brush and grass.

"Range No. 7 may not make a covey the first year, but it may be depended on for the second.

"*Covey No. 8.* The east end of the draw in the ungrazed woodlot, at the south-centre of the farm, offers a south-facing bank which may be treated the same as 2*a*, but range 8 differs from range 2 in this respect: it is surrounded by permanent pasture, instead of corn. It is the only one of the present or prospective ranges which lacks food. Accordingly a narrow bench along the draw should be cleared and plowed up and planted to sorghum, or some other small grain not requiring much cultivation. Shock half of this and open a new shock with each snowstorm. This food-patch will insure an eighth covey, especially if a boundary 'fence' of uncut timber is left between range 8 and range 2.

"To sum up: Within 2 years after rebuilding this farm for quail it should carry annually thereafter 8 coveys instead of 2. Eight coveys at 15 each would be 120 birds on 170 acres, or 1.4 acres per bird. This will be a very fair stand.

"The rotation of crops on the farm may leave certain ranges cornless during particular years, but this loss will be offset by new corn in new possible covey locations, or can be artificially offset by food patches."

GAME SURVEYS

Definition. The term "game survey" is being used to designate two quite different things: (1) current annual "crop reporting" as a basis for current regulatory measures; (2) an appraisal of the trend of productivity factors, and a forecast of policy measures necessary for game restoration.

The term is here used in the latter sense. "Crop reporting" is really a rough annual census rather than a survey, and is covered in Chapter VI.

In the sense here used, and at the present time, a game survey is an attempt to change the orientation of thought and action on wild life conservation; to point out, in terms of local game species, and local game range, the difference between the old concept of retarding the diminution of a dwindling resource, and the new concept of cropping and building up that resource through environmental controls. However much individual ideas may differ on questions of method, there remains a fundamental distinction between the old idea of hoarding, and the new idea of building. Local people can see this difference when the new idea is expressed in terms of proposed changes in their own land, laws, and customs.

Obviously no "game survey" can of itself transform the public mind, but it can, if rightly executed, mobilize and activate the forces which hasten the rate of change, and influence their direction.

Functions. Any useful change in public attitude toward game must be built upon a better public understanding of what determines game abundance. The average citizen still thinks that:

Abundance = (laws + artificial restocking + vermin control) − shooting.

The first function of a game survey is to point out the inadequacy of this popular formula, and the fallacy of some of the policies deduced from it. The survey must amass actual historical evidence to show how agricultural and forest practice, by influencing food, cover, or other factors, has nullified restocking or made "vermin" control irrelevant. The past history of the land, the game, and the laws must be reconstructed, and their trends projected into the future.

A second and more difficult function is to show what would happen if landowners regulated shooting and took care of game environment. To remove this question from the realm of mere conjecture, places must be found where one or both of these things happened *accidentally*, and some kind of comparative measurements of their effect on game built up.

Who is the future landowner? The surveyor must project into the future the trend of economic changes in the land-owning industries, and the land program of related conservation activities such as forestry and parks. From these he must forecast some give-and-take adjustment which will fit each of them and also the needs of game. His mind, if not his report, must contain some sort of picture of a future system of land use.

A fourth and much easier function is to demonstrate our present biological ignorance. Actual cases of mis-appraisal of conservation questions due to misunderstanding of the relative strength of biological forces can be found by the dozen in any state, together with the historical evidence to prove them.

More difficult is the planting of a conviction that research can gradually dissolve this ignorance, and that local institutions can and should undertake such research. The surrounding territory may furnish actual examples.

The local public almost invariably expects a survey to recommend changes in appropriations, laws, and administrative organization. It is usually necessary to show that what administrators *think about* is more important than how they are organized, or how much money they have, or what laws they work under.

Demonstrations. Surveys are usually expected to recommend policies rather than to initiate actions. In the field of game, however, it seems doubtful whether theories and plans alone, no matter how well supported by evidence, are nearly so useful as samples or demonstrations of how those theories and plans work out in practice.

The effect of environmental controls by the landowner, for instance, can be tested by actual trial on a land unit typical of the area being surveyed. The utility of research can likewise be tested. Both kinds of demonstrations commonly begin to yield significant results within a couple of years. A real game survey should be given (or should seek out) the funds necessary to initiate such a demonstration to test each of its major findings. The public, within a short period, can thus judge those findings by the way in which they work. The development plan shown in Fig. 33 is for a quail demonstration area in Iowa.

Personnel. It is usually footless to make a game survey without at the same time training personnel which will know how it was made, which will know what it means, and which will remain in the locality to follow up and execute its findings. If the locality is a state, this means that the surveyor should have as his "first lieutenant" a carefully selected man who will continue in a position of leadership in the state.

History and Trends. The history of game and of changes in land-use can be partly reconstructed from the local biological and agricultural literature, which must be pretty thoroughly reviewed in advance. A wealth of less accurate but nevertheless useful detail can be hung upon this framework by compiling the recollections of local people. Diaries and journals of sportsmen and naturalists, the books of former commercial game dealers, official reports on various land industries, weather records, statutes, old files of sporting and agricultural periodicals, and a multitude of other sources of information lie ready-to-hand. The problem is to make a good guess as to which are worth skimming.

All of this bears on reconstructing the past. Probable future trends in land industries are usually quite definitely forecast by agricultural colleges, forest schools, official departments, and private organizations for the promotion of this or that activity, and can be obtained from their reports and their specialized personnel.

Finally, a practical understanding of the customs, prejudices, enthusiasms, and social outlook of the people must be picked up in the course of the survey, and the immovable points carefully charted. The future course to be recommended must steer around and between these fixed points, or the survey may end up as merely "a new book for the library."

The surveyor, however, cannot afford to be merely "a lute on which all winds can play." His historical conclusions and his estimate of trends must be constantly checked against that greatest but least-read of all books: the face of the land.

It is astonishing how few of those who have learned by rote rule or "nature study" the *statics* of the land's present inhabitants or condition, ever learn to read the *dynamics* of its past history and probable future. To see merely what a range is or has is to see nothing. To see *why* it is, how it *became*, and the direction and velocity of its changes—this is the great drama of the land, to which "educated" people too often turn an unseeing eye and a deaf ear. The stumps in a woodlot, the species age and form of fencerow trees, the plow-furrows in a reverted field, the location and age of an old orchard, the height of the bank of an irrigation ditch, the age of the trees or bushes in a gully, the fire-scars on a sawlog—these and a thousand other roadside objects spell out words of history, and of destiny, of game and of peoples. They are the final authority on the history of the recent past and the trend of the immediate future. How to read such evidence is not easily set down on paper. Some of the forestry literature may be suggestive (Leopold, 1924 and 1924*a*).

Biological science, if it had no economic import at all, would nevertheless be justified by its enrichment of the human faculty for observation. Jason, Eric, Magellan, Daniel Boone, saw only the cover of the Great Book. Its free translation is the unique privilege of post-Darwinian explorers. To this first generation of game managers, especially, is offered many a virgin page.

This completes our analysis of the mechanism of game productivity, of the factors which determine it, and of the available means for their control. These three subjects constitute the theory and technique of management.

There remain to be sketched some of the reasons for perpetuating a game supply, some of the incentives for securing the widespread practice of management, and some standards for evaluating the results. A brief discussion of how to prepare for a professional career, and of prospective opportunities in it, is also added.

No exhaustive treatment of these questions seems appropriate in a volume devoted primarily to principles and technique. Only enough is given to afford a starting point for the reader's own deliberations. A larger element of personal opinion, not supportable by tangible evidence, is necessarily injected into these final chapters.

PART III

GAME ADMINISTRATION

Chapter XVI

GAME ECONOMICS AND ESTHETICS

What Is Sport? For unnumbered centuries physical combat between men was an economic fact. Battle was part and parcel of the daily struggle to get, or to keep, a place in the sun. As the economic need for battle became more and more occasional, it was delegated to specialists. But the instinctive zest for physical combat did not disappear. Hence athletic sports and games.

Physical combat between men and beasts was likewise an economic fact. Since first the flight of years began, it was part and parcel of the daily business of getting something to eat. Gradually agriculture and commerce supplied other and better means of subsistence. But the hunting instinct, the love of weapons, the zest in their skillful use, did not disappear with their displacement by economic substitutes. Hence sport with rod and gun.

Socially speaking, these surviving sports are an improvement over their economic antecedents. Football requires the same backbone as battle, but avoids some of its moral and physical retrogressions. Hunting for sport is an improvement over hunting for food, in that there has been added to the test of skill an ethical code, which the hunter formulates for himself, and must live up to without the moral support of bystanders. That the code of one hunter is more advanced than that of another is merely proof that the process of sublimation, in this as in other atavisms, is still advancing.

The hope is sometimes expressed that all these instincts will be "outgrown." This attitude seems to overlook the fact that the resulting vacuum will fill up with something, and not necessarily with something better. It somehow overlooks the biological basis of human nature,—the difference between historical and evolutionary time-scales. We can refine our manner of exercising the hunting instinct, but we shall do well to persist as a species at the end of the time it would take to outgrow it.

Recreational Values. The wild-life conservation movement is an attempt to prevent our expanding population from destroying its own opportunities for sport.

Management is a way to maintain a supply of game, and other wild life, in the face of that expansion.

But it is not merely a *supply* of game, in the strictly quantitative sense, that is in question. The conservation movement seeks rather to maintain values in which *quality* and distribution matter quite as much as quantity.

Like most other really important things, this conception of quality eludes easy definition. We might, if we chose to spend the money, release each year millions of artificially reared birds, and thus "maintain" a supply of game in the quantitative sense. But would we thus maintain value? I think not.

Intensity of Management and Population Density. It is evident throughout the preceding chapters that game management may exert various degrees of control over the factors of productivity. The greater the degree of control, the denser the stand of game, and the larger the crop which may be removed.

There is a definite relationship between the necessary intensity of management and human population density, which may be illustrated by a comparison:

The Scottish grouse moors support about one grouse per three acres on the average, and one per acre as a maximum. This is a very dense stand, obtainable only through intensive management.

The Wisconsin grouse moors, which we prosaically call "the sandy counties," support about 1 grouse per 40 acres. This is a very thin stand, occurring "naturally" without any management at all. Section (*b*) of Fig. 34 contrasts the two.

A crude or extensive system of game management would raise the Wisconsin grouse density to (let us say) one per eight acres, or five times the present stand. On the other hand, a complete or intensive system of game management would doubtless raise it to that of Scotland, or 20–40 times the present stand.

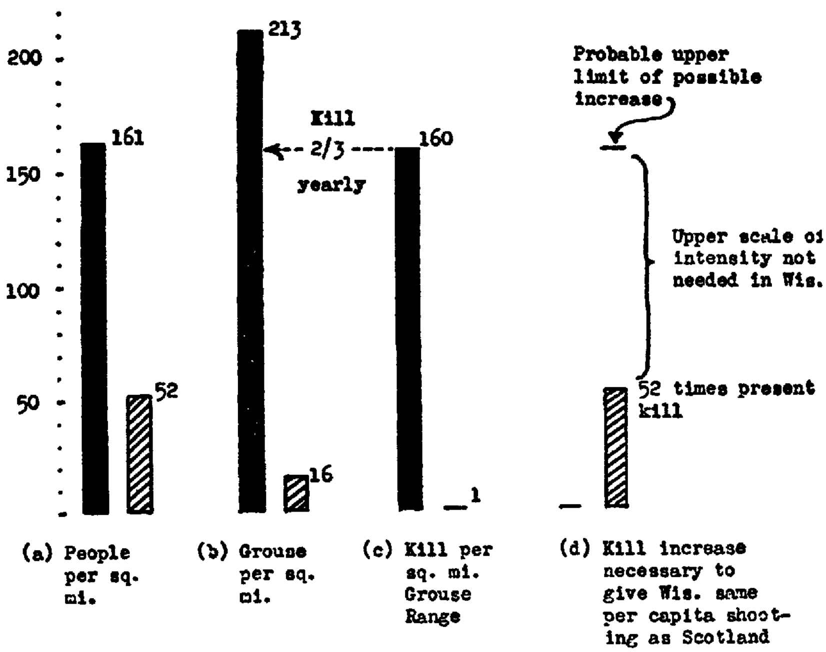
As nearly as we now know, disease would frustrate any attempt to raise the density higher than this in either place.

There has been no management in Wisconsin grouse so far, because until recently its citizens were able, by reason of their low human population density, to get grouse hunting without it. The comparative human population densities appear in Section (*a*) of the chart.

We are working, therefore, between an upper limit set by biological nature, and a lower limit set by economic accident. Art

FIG. 34

Populations of People & Grouse in Scotland (■) & Wisconsin (▨)
In Relation to Intensity of Management   Aldo Leopold 3-23-31



cannot raise the upper limit. Delay can depress the lower, and exterminate the species. The two limits constitute the upper and lower edge of our game policy "slate." The two limits are far apart. Between them lie a wide range of alternatives, among which we are free to choose, subject only to the general rule that the intensity of game management must go up as human population density goes up. In sparsely settled communities no management is needed. In very densely settled communities the limit which the land can be made to carry must be sought.

Intensity of Management and Yield. The denser the stand of game, the larger the proportion of it which may be safely killed. In fact, in Scotch grouse stands nearing the upper limit of density, it is considered imperative to kill two-thirds. On the other hand, in Wisconsin grouse stands, probably nearing the lower limit of survival, it is probably more or less damaging to kill any at all.

If Wisconsin's present stand permits of a 40-fold increase, her present kill could be raised much more than 40-fold. Section (*c*) of the chart would indicate 160-fold.

Five Theorems. From these biological premises may now be deduced five theorems which approximately express the relationships between recreational value, game density, and human density:

1. *The denser the human population, the more intense the system of game management needed to supply the same proportion of people with hunting.*
2. *The recreational value of a head of game is inverse to the artificiality of its origin, and hence in a broad way to the intensiveness of the system of game management which produced it.*
3. *A proper game policy seeks a happy medium between the intensity of management necessary to maintain a game supply and that which would deteriorate its quality or recreational value.*

The third theorem as applied to Wisconsin, or America, means that a game policy should seek a happy medium between the evident necessity of some management, and the esthetic desideratum of not too much. We would be foolish not to take advantage of our relatively low human population density as compared with Europe. On the assumption that about one-third of both Wisconsin and Scotland constitutes grouse range, and that on this range the Scotch kill of 160 grouse per square mile could, with intensive management, be duplicated, to what degree would it need to be duplicated to furnish Wisconsin citizens with the same per capita opportunity for shooting as Scotland? Section (*c*) indicates a 50-fold increase in kill would suffice. This, I estimate, would call for about a 6- or 10-fold increase in the stand.

Wisconsin's total kill could doubtless be increased 160-fold before reaching the biological upper limit. In short, we need to use only one-third the possible scale of intensity of management (see Section *d*).

If we ever have as many people per square mile as Britain, we too will be forced to practice intensive methods, or do without our shooting. This raises the interesting question of whether, having automatically filled up the biological niche which Columbus found for us, we will prove capable of regulating our future human population density by some qualitative standard. Or will we just leave it to Mr. Ford to "manage" us on the general principle of the more the merrier? I fear we will. The boosters fear we will not, or that there may be some needless delay about it.

Some, but not too much, management is good esthetics, but is it also good business? Game management is a form of agriculture. Does it, like the other forms, obey the Malthusian law of diminishing returns? That is to say, does a dollar or an hour spent in quintupling the present accidental stand of grouse go farther than a dollar spent to quintuple it again? We would then be approaching the biological upper limit of density, where it may take more "work" to add a bird than lower down on the bioeconomic "slate."

I think this is true of game *stands*. Whether this would also be true of yields or kill may be doubtful, because in game, yield increases more rapidly than density. We have had so little management in this country that we must leave this point in doubt. Time may show *cheaper costs for the lower scale of game populations, and if so, this will constitute a fourth theorem.*

This tentative theorem has an important corollary which is probably true within certain limits: A dollar spread over a large area will raise more game than the same dollar spread over a small area. This is overlooked by those who entertain the illusion that the state can "raise game for all" on small public shooting grounds. It is also overlooked by those game farmers whose operations have been confined to private estates whose owners want lots of shooting on their own small area, regardless of cost.

Another theorem can be set down with entire confidence:

5. *Only the landholder can practice game management cheaply.*

The reason is that game management normally consists of many small jobs scattered through the whole gamut of the seasons. The farmer or forester can perform these jobs "on the side," often without any separate cash cost.

The American Game Policy sketches in broad outline the present application of these five theorems to American management. It proposes low-intensity management on all lands (rather than high-intensity management on a few spots) in order to take advantage of the lower costs and lesser artificiality thus obtainable. It proposes that the public be its own manager wherever it can own the land, but admits the necessity of working through the private owner where it cannot. No policy, of course, can map an exact route to these objectives. The details of the route must be worked out a step at a time by "try and see" procedure.

The Trend to Naturalism. The viewpoint underlying the five theorems is not merely one of driving a good compromise between economic conditions and esthetic ideals. It is grounded in sound biology as well, and applies not only to game management, but to all fields of conservation. In forestry, this viewpoint has been called "naturalism." The term carries its own definition: It is an effort to avoid artificiality in the manipulation of natural processes for conservation purposes.

For a century the whole world sought to emulate the artificially planted spruce forests of Germany. Their absence of competing hardwoods, their astonishing yields, their long black rows of dense, even-aged trees, were held up as a model of "efficiency." Suddenly the soil turned "sick"—of too much spruce. Insect pests swept through the unbroken stands like a forest fire. Today the Germans are seeking the beneficent fertilization of beech trees and other hardwoods; cuttings are made selectively as in nature; natural reproduction instead of artificial planting is becoming the rule. Artificiality failed in the long run.

In planting conifers, foresters have always spaced the young trees closely, so that they would prune each other. Three or four times as many were planted as could possibly mature. Hardwood brush was regarded as an impediment to be destroyed in advance, if possible. Stafford (1931) now proposes "skeleton planting," in which only the final stand is planted, and the natural competition of hardwoods utilized to do the crowding and pruning, and incidentally to fertilize the soil. Here again we return to an approximation of nature. We still manipulate, but in a nearly natural instead of in a largely artificial manner.

The forest-fire evil in many regions is partly the result of unnaturally large and complete openings in the forest canopy.

"Selective logging" offers a partial remedy applicable to shade-tolerant species. Selective logging is natural logging.

In the field of watershed conservation and flood-control there is a definite issue between the engineers who tend to rely on engineering works alone, and the foresters and biologists who insist that vegetative cover and soil fertility are indispensable adjuncts to dams and dykes. The latter viewpoint is the naturalistic one. It is strongly supported by current research findings.

The present controversy over methods and degrees of predator-control involves the issue of naturalism, as well as other issues.

In European game management there is a perceptible revival of naturalistic practices. Maxwell (1913) describes several English estates where the pheasant is successfully produced wholly by *wild* management, as distinguished from artificial propagation.

Fish management has heretofore relied wholly on artificial replanting of fry raised in hatcheries, or even replanting of mature fish. Hubbs (1931) is now developing environmental controls for Michigan trout streams and lakes, which promise to reduce the need for artificial replanting.

The movement to establish permanent wilderness areas in the National Forests and Parks, to be devoid of motor roads, resorts, or other "improvements," is perhaps the most salient manifestation of naturalism so far apparent in conservation affairs (see Leopold, 1925*a;* Marshall, 1930).

Merely negative protests against economic encroachments, and their aftermath of artificialized conservation, are of course no new thing. They are different from and far less significant than the positive remedial actions here mentioned. Salty tears flow easily, but workable ways to save men from their own success come hard. The game manager must handle his share of this great social problem.

Production Incentive. Game being a low-cost low-yield crop, which can be produced cheaply only by the landholder in conjunction with his other cropping operations, it follows that many landholders—if possible, *all* holders of suitable lands—should be induced to practice management.

Some will find sufficient inducement in the personal pleasure, or the opportunities for hospitality, to be derived from the crop of game.

Governments, in so far as they can own land, will find sufficient inducement in the fact that a game crop promotes the public welfare.

No conceivable system of private preserves and public shooting grounds, however, could adequately accommodate the growing army of urban citizens who like to hunt. The non-shooting landholder must also be induced to manage his game. The only conceivable motive which might activate a sufficient number of non-shooting landholders is the financial motive.

Why All the Land Must Produce. What is "a sufficient number?" Let us work out this basic question in concrete figures for Iowa, a state of average population density, extra favorable soil, and offering relatively accurate basic data by reason of the recent game survey made there. I select pheasants as an example, not because this species is the most important, but because the Iowa pheasant range is the most homogeneous I know of, hence the acreage available for production can be accurately calculated without a detailed type map.

Fig. 13 shows us that the northern half of Iowa is proven to be actual or potential pheasant range. The area of the state is 35,000,000 acres, hence the prospective pheasant-producing region has a gross area of about 17,000,000 acres. By reason of the extraordinary homogeneity of the range, we need deduct as blanks only towns, rivers, highways, etc. There are probably 14,000,000 acres for potential production.

The present census shows clearly that the best stands run between one and two acres per bird, but even under management we can hardly hope for an *average* stand of more than a bird per four acres. This is many times the present average. Table 22 indicates that under management not to exceed half may be safely killed. It therefore requires 8 acres to produce a pheasant "in the bag." Our available area will therefore produce a kill of $14{,}000{,}000 \div 8 = 1{,}750{,}000$ pheasants annually.

About 170,000 hunting and fishing licenses are issued. Assuming that this represents the social need for hunting facilities, the soil of Iowa is capable of growing for each licensee an annual kill of $1{,}750{,}000 \div 170{,}000 = 10$ pheasants, *if every landholder within the proven range practices management.*

No similar calculation of like accuracy has probably yet been made in this country.

Is there, then, any chance to perpetuate hunting as a sport on *a small fraction* of the proven range? Can anything but the financial motive be relied upon to activate a *large* fraction?

Ways of Marketing Game Crops. The evolution of orderly mechanisms for marketing of game crops, and thus activating the financial incentive to produce them, has just started in this country. The differences in land-tenure and political ideas make the European mechanisms hardly applicable without modification.

The American Game Policy outlines in some detail the possible ways of marketing game crops, sets up criteria whereby their merits and demerits may be judged, and describes some of the current attempts to use them.

Management Costs and Revenues. The items of cost in producing a game crop are land, labor, and materials. Costs are subject not only to the ordinary variants affecting all land-cropping operations, but likewise to differing conditions of land tenure which determine:

1. Whether the game, or some other crop, carries the interest and taxes on the land.
2. Whether the game, or some other crop or use, carries the labor and supervision.
3. Whether the owner is a tax-exempt government, or a tax-paying private citizen or group.

A farmer raising game as a by-product may legitimately charge against the farm crop, rather than against the game, all costs except land deliberately withdrawn from profitable farming, and labor or materials especially purchased for game purposes. The waste corners devoted to game cover, the waste grain serving as food, and the odds and ends of time used in care of game, are all items for which he would get no return, even if they were not used for game production. Such a farmer can produce game at a very low cost, or often at no cost at all.

On the other hand a private game preserve, acquired for game purposes alone, must charge all costs of land, including taxes, and all labor and materials, against the game crop. If the land must be farmed at a loss to make it produce game, or if artificial propagation is used, the costs may run very high.

An intermediate case is the public forest which pays no taxes.

The cost of acquiring the land is charged against the timber crop. The game need carry only the special personnel and materials used in its production.

Migratory game projects, such as duck clubs, present a special case, in that they rarely produce their own game, but rather draw on a mobile public supply. Costs are usually limited to land, supervision, and "improvements." Costs are sometimes very high, but usually by reason of the strategic location of the land, or special measures used to make it attractive. Once in a while, though, one finds a duck club which has invested large sums, not merely in attracting the public's ducks, but in *producing* a far larger number than it kills. A group of such clubs is convincingly described by Day (1932).

Another special case is that of the state which is attempting to practice management on lands which it does not own. It escapes all land costs, except occasional public refuges, all labor costs except a limited degree of patrol and artificial propagation, and all costs for materials except occasional feed bills. Its costs are exceedingly low (and so are the resulting crops).

Table 53 shows the probable distribution of "contributed" and "special" cost items under several typical conditions of land tenure.

The meaning of the preceding discussion, boiled down to a single sentence, is this: The farmer has a special economic advantage in game production costs.

With this background, the meaning of such few actual cost figures as are available can be made clear.

No cost figures for Case *A*, based on actual experience, are as yet available. Careful estimates of food and cover changes based on range development plans of the sort depicted in Fig. 33 are as follows:

Quail, 170-acre farm	13c. per acre per year.
Pheasants, 1920 acres	3c. per acre per year.

In both instances the improvement costs, such as fences, are spread over five years, and commercial rentals are charged against land withdrawn from plow or pasture. No labor costs for supervision or patrol, however, are included. In general, it seems safe to say that unless the farmer spends cash for artificial propagation, or withdraws productive land from agricultural use, he has

Table 53

EFFECT OF LAND-TENURE ON GAME COSTS PER ACRE

Case, Costs	A Farmer	B Private Game Preserve	C Public Forest	D State or Private Land	E Lumber Company
Land					
Rental or purchase	C	X	C	none	C
Taxes	C	X	none	none	C
Labor & Materials					
Supervision	C	X	C	X	X
Cultivation	C	X	X	C	X
Patrol	C	X	C	X	C
Feeding	C	X	X	X	X
Coverts	C	X	C	C	C
Predator control	C	X	X	X	X
Artificial propagation	X	X	X	X	X

Legend: C = contributed by some other crop or use.
X = special expense.

practically no costs, and any revenue he can get from game is virtually net profit. In the case of farm co-operatives engaged in game management, there is usually a cash cost for patrol, and in the future there may be costs for technical supervision.

One variant of Case *A* is the country estate, owned for residence purposes, but producing game as a side issue. Such estates, having a limited area and no pressing need of keeping costs down, commonly resort to artificial propagation. Country estates in the New York region, producing pheasants artificially, spend as high as $5.70 per acre per year. This includes no charges for land, but only food crops, propagation, and game personnel. In a typical case the cost per bird turned down was $3.20; the cost per bird brought over the guns was $4.75. Certain revenues were realized by the sale (legally tagged) of the kill at $1.75 per bird. (See Curtis, 1928.)

Case *B* (private game preserves) is represented by the numerous quail preserves in the South, which own or lease land for quail production. Cost figures on six such preserves show that they spend quite uniformly 5–10 cents for land rental, and 10–30 cents for labor and materials, total 15–40 cents per acre per year.

Land rentals sometimes run up to 15 cents. Since it takes several acres to yield one quail yearly, a quail "in the bag" costs them about $1 for management, where all the costs are charged against the game. (On going farms in the same region, representing Case *A*, where game is a by-product, a quail in the bag should, of course, cost very much less.)

Hungarian partridge management on a typical English manor, where shooting privileges are leased from small farmers and management conducted by a separate gamekeeper personnel, costs about 22 cents, 12 cents for land rental and 10 cents for operations (Page, 1924). Such manors average about 6,500 acres, with 50 per cent or more plowland. They yield a bird per 3–8 acres, and average a bird per 5 acres. Hence the bird "in bag" costs $1 or a little more—about the same as quail in the South.

An example of Case *C* is a National Forest, which the federal government owns and administers for timber production purposes, but the game on which is owned by the state. Management is a co-operative enterprise, conducted by the state and federal officers. Shooting is open and free to the public under the state laws. Because of the huge area of such forests, expenditures per acre are low, but commonly well directed. Supervision and patrol (time of forest officers actually spent on game work) run around 1/50 cent per acre; predator control 1/20–1/5 cent; fire control ½ cent. Part of the predator control is properly chargeable to livestock, and of fire control to the timber crop. The total gross expenditure for game is well under ½ cent per acre per year. The yield is very low. On the Gila National Forest in New Mexico, during the 5-year period ending in 1928, the yield was 1 buck per 2500 acres, and 1 turkey per 32 square miles.

Another example of Case *C* is the Pennsylvania public shooting ground system for big game. A "primary" deer refuge of 2500 acres costs about $35,000 to buy, plus $375 per year paid the county in lieu of taxes. It serves roughly 25,000 acres. If the annual cost of the refuge and its keeper is prorated over the area served, the land rental chargeable to game would be 8½ cents for the area served. Supervision of such a unit costs ⅘ cent, patrol and fire 8½ cents, covert improvements ¾ cent, total 20 cents per acre per year. The yield of such units is about 1 buck per 220 acres. A buck "in bag" thus costs the state over $15.

Case *D* is represented by the average state game department which attempts to practice management on private lands without the assured co-operation of the owner. The cost is the budget of the department divided by the area of the state. One or two states spend one cent per acre in this manner; most of them much less. The expenditure is largely for patrol (law enforcement) and restocking with game raised on state game farms. Pheasants 8–10 weeks old produced on state game farms cost at the point of release from $1.28 upward. The usual cost is over $2.00. Since the average license yields less than the cost of planting a single bird, and since the licensee is legally entitled to kill many birds, it is readily apparent that the ultimate solvency of the system depends on a strong natural increase in the birds released. This is possible only on managed range, or where the condition of the range has accidentally remained favorable.

No data are available on Case *E*.

Management of Other Wild Life. The objective of the game management program is to retain for the average citizen an opportunity to hunt. As already pointed out, this implies much more than the annual production of a shootable surplus of live birds to serve as targets. It implies a kind and quality of wild game living in such surroundings and available under such conditions to make hunting a stimulus to the esthetic development, physical welfare, and mental balance of the hunter.

The objective of a conservation program for non-game wild life should be exactly parallel: to retain for the average citizen the opportunity to see, admire and enjoy, and the challenge to understand, the varied forms of birds and mammals indigenous to his state. It implies not only that these forms be kept in existence, *but that the greatest possible variety of them exist in each community.*

In times past both of these categories of opportunity existed automatically, and hence were lightly valued. Both are now, by reason of their growing scarcity, perceived to be immensely valuable. Conservation is nothing more or less than a purposeful effort to perpetuate and extend them as one of our standards of living.

Experience with game has shown, however, that a determination to conserve, even when supported by public sentiment, protective legislation, and a few public reservations or parks, is an insufficient conservation program. Notwithstanding these safeguards, non-game wild life is year by year being decimated in numbers and restricted in distribution by the identical economic trends—such as clean farming, close grazing, and drainage—which are decimating and restricting game. The fact that game is legally shot while other wild life is only illegally shot in no wise alters the deadly truth of the principle that it cannot nest in a cornstalk.

Only a decade ago it was considered a profundity to assert that wild life harbored in the forest, and that the conservation of forests would solve the wild-life problem. Next we complicated the situation by realizing that quail need brush, prairie chickens grass, and grouse forest. Now, after some research, we can talk about quail as occurring wherever an acre of tall bluegrass interspersed with coralberry occurs between ungrazed brushland and corn, provided it be not a north slope.

Measured by its effectiveness, this new formula is worth 10,000 platitudes about forests and wild life. The crying need at this stage of the conservation movement is *specific definitions* of the environment needed by each species.

This is just as true of songbirds as of game. Consider the effectiveness of the recent specific definitions of winter feeding methods for each species, and compare them with the old romance about "bread crumbs on the windowsill." Compare the modern bird house, designed to fit the species, with the gingerbread castles of former years. Songbird conservation has progressed in these respects, but in other respects it has stagnated. We still lack definitions of what constitutes habitable range for those numerous and valuable forms which need neither nesting houses nor artificial feeding.

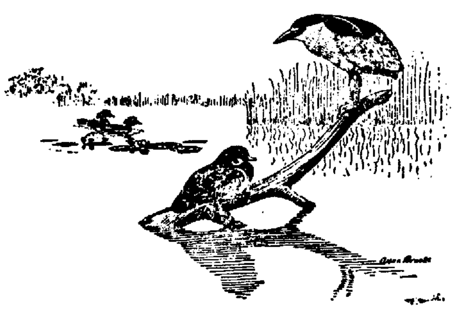
Building Environments for Songbirds. A pair of wood thrushes is more valuable to a village than a Saturday evening band concert, and costs less. What does it cost? A piece of woodland with undergrowth. What kind and size of trees? How many acres? What undergrowth? Does it matter what surrounds the woodland? Can it be grazed? Must it contain water? What other species help, or hinder, its occupancy? Research in applied ornithology is just as capable of answering these questions, not only for wood thrushes but for a hundred other species, as the equivalent questions for quail or pheasants.

Environments can, by the judicious use of those tools employed in gardening or landscaping or farming, be built to order with assurance of attracting the desired bird. In short, by deliberately and intelligently reversing the processes which are destroying bird environments, we can restore not only birds in general, but those particular birds in which the landowner may have a special interest.

This is the substance of game management, and can likewise become the means whereby each community creates its own dearth or abundance of non-game birds. Is it not probable that landowners who now proudly exhibit their bird baths or feeding stations will be equally enthusiastic about the diversity of bird environments which they can build up? Should not public parks be "landscaped" with an eye to the variety of their bird life, as well as to the beauty of their scenery?

The realization of this idea awaits only specifications. Scientific institutions now busy with Sumatra or Galapagos should consider this virgin field of opportunity which borders their own campus. As in game management, systematic observations, followed by trial modifications of the environment and measurement of population response, are the technique to be used.

There is, in short, a fundamental unity of purpose and method between bird-lovers and sportsmen. Their common task of teaching the public how to modify economic activities for conservation purposes is of infinitely greater importance, and difficulty, than their current differences of opinion over details of legislative and administrative policy. Unless and until the common task is accomplished, the detailed manipulation of laws is in the long run irrelevant.



Chapter XVII

GAME POLICY AND ADMINISTRATION

Definition. Game management has already been defined as the art of producing sustained crops of game for recreational use.

Game administration is the art of governing the practice of game management. Its function is to encourage management by fact-finding, demonstration, and education, and to regulate abusive practices. Incidentally, governments may themselves practice management on government lands.

Game policy is the plan of administration adopted by government.

Function of Government. Actually, game administration in this country has so far concerned itself almost entirely with two things: regulating abuses by the exercise of its police powers, and attempting to practice management on private lands without the co-operation of the owner. The latter attempt is bound to fail in the long run, because government cannot control environment on lands which it does not own. It can plant game on them, and to a very limited extent (by fixing seasons and bag limits) regulate the kill, but these alone are seldom sufficient to produce a sustained crop.

Experience, if not cerebration, will inevitably tend to shift the emphasis in game administration to its true functions. In agricultural administration, government does not try to plant or harvest crops on private lands, as it does in game. It does, however, maintain great agricultural colleges and a network of experiment stations to discover better cropping technique, and a nation-wide system of agricultural extension agencies to tell the farmer how to use these discoveries. Game administration must install a similar machinery for research and education, or else use the agricultural machinery already set up. Since game is largely an agricultural by-product, the latter course seems by far the best.

Evolution of Administration. Under this conception, a state game warden is not primarily a policeman and a game-farmer (as he is now usually considered). He is first of all a co-ordinator of game research in state institutions, and an organizer of education in game management. He acquires public lands and directs game management on them. He formulates policy for the regulation of private practices on private lands. Incidentally he formulates and enforces game laws, just as the Secretary of Agriculture incidentally handles quarantines. He uses public game funds for the furtherance of all these functions. In short, he is a statesman charged with the duty of guiding the operation of economic and social forces in a highly technical field. Obviously he must either be a technician himself, or know how to use technical and scientific men to good advantage.

The history of game administration in this country clearly shows that it follows the same basic sequence of ideas already described in Chapter I. The successive stages of progress are:

1. Policing the remnants of the virgin game crop.
2. Undertaking game farming (artificial replenishment).
3. Acquiring state lands and managing them.
4. Starting educational work.
5. Starting fact-finding work after learning that the requisite facts for 2, 3, and 4 do not exist.
6. Starting to encourage private management. Regulating private management in the public interest.

Some of our states have just entered stage 2. Others have reached stage 5. None has as yet seriously entered upon stage 6.

The kind of laws, the kind of personnel and salary scales, the scale of finance, and the degree of discretionary authority suitable for the first function is of course entirely unsuitable for the last. Hence the prevalence of popular "campaigns" to reform and reorganize conservation departments.

Organization of Conservation Departments. Experience seems to show that no particular form of organization has any inherent merit in and of itself. Merit lies only in personnel, and any particular form is good or bad only in so far as it provides a good or bad mechanism for the personnel to work with.

It is doubtful whether, with a given personnel, one form of organizing is much better than another, providing each scores reasonably well on the following criteria of effectiveness:

1. Discretionary and regulatory authority.
2. Continuity of policy.
3. Co-ordination of activities

Each of these criteria is the antithesis of the condition prevalent under the domination of partisan politics. Each, except the first, can be achieved by good personnel alone, if that personnel is allowed to work through a sufficient period of time.

Some type forms of state game organization are described in the *Game Survey* (p. 238). A form called the "Commission-Director" type is now much in vogue. It was originally patterned after the "Board-Manager" or corporation type in industry. History shows, however, that the mental outlook and calibre of the *personnel* quickly *bends to its own pattern* whatever legal framework is set up.

Preoccupation with form of organization pervades popular thought on federal as well as state administration of conservation affairs. There is a latent movement for the amalgamation of all federal conservation activities under a single head. This would be fine if "conservation activities" had any sharp boundary, and if they could be dissociated from the economic activities necessarily conducted on the same land and headed up in various federal departments. That they have no such boundary and that they cannot be dissociated from economic uses, is evident on nearly every page of this book.

The whole question of how to organize public administration boils down to this: Get the personnel and they will build their own "house." To the extent that "reorganizations" and "house-cleanings" help to get or keep able personnel, they are good. To the extent that they are relied upon to make poor personnel better, they are a delusion.

It is, of course, idle to expect to keep able personnel, even in a soundly organized department, unless the salary scale is comparable to that of an industrial enterprise of like magnitude. This, so far, is seldom the case. A vigorous transition from a political to a technical administration in the course of time often carries with it substantial improvements in salary scale. The transition in the U. S. Forest Service, described in the next chapter, is a case in point.

Legal Status of Game. Taverner's theory that the first game laws were evolved from tribal taboos has already been pointed out in Chapter I.

The legal foundations on which our present system of game administration is founded are succinctly outlined in *Wild Game*

—*Its Legal Status* (1931). The quotations which follow are taken from this publication.

"From the earliest traditions the right to reduce (wild) animals to possession has been subject to the control of the law-giving power.

". . . 'Solon, seeing that the Athenians gave themselves up to the chase, to the neglect of the mechanical arts, forbade the killing of game.'

". . . things were classified by the Roman law into public and common. The latter embraced animals *feræ naturæ*, which, having no owner, were considered as belonging in common to all the citizens of the State."

". . . Justinian recognized the right of an owner of land to forbid another from killing game on his property."

"After the Norman Conquest and before the Magna Charta of King John, it seems that the ownership of wild game in England was vested in the English King . . . in his individual capacity and as a personal prerogative.

". . . when the barons at Runnymede exacted from King John the Magna Charta in 1215 a change seems to have taken place. . . . Since then, it has become established that the King owns all the wild game . . . in his sovereign capacity . . . in 'sacred trust' for the people. This principle forms a part of the common or unwritten law. . . .

"The colonists who settled in America carried with them the common law of England. After the American Revolution . . . the State acquired the title of the King, and so it has been held uniformly in this country that the wild game is owned by the State in its sovereign capacity in 'trust' for the people of the State.

". . . it follows that an individual cannot obtain an absolute property right in such game except upon such conditions, restrictions, and limitations as may be permitted by the State. . . . The conditions . . . are . . . within the province of the Legislatures. . . ."

"While the State has an ownership of the wild game within its borders, the individual owner of real estate has an interest in the game on his premises. This interest is not an absolute property right, but is in the nature of a qualified property interest in such game. No other person has a right to go upon his premises, without permission, to take the game. Subject to the regulations imposed by the State, the owner of the land has the right to control the game on his lands."

The foregoing passages clearly trace the history and nature of public and private property in game, as founded on the common law. The frequent allusions in American literature to the different ownership of game as between America and England refer to different *degrees* of "conditions, restrictions, and limitations permitted by the State," and not to any basic difference in allocation of title.

Some additional quotations of special interest are the following:

"Another ground frequently advanced to support the right of the Legislature to impose regulations governing the hunting of wild game is the police power. Under the police power a State has power to regulate in the interests of the public health, safety, morals, and welfare."

". . . a hunting license granted by the State to an individual, even if it purports to do so, gives the holder of the license no right to invade the private hunting grounds of another person."

"Although a person has no natural or inherent right to hunt on the premises of another, a right to so hunt may be acquired by grant from the owner."

". . . an action of trespass may be brought by one who owns the exclusive right to hunt on certain lands, although he does not own the fee."

"The public have a right to resort to public waters and take fish or shoot water fowl. . . . In the case of private waters the public have no fishing or fowling rights. . . . Even in the case of public waters a hunter must not pass over private property to reach the public shooting grounds."

Game Policy. The Experimental Idea. As long as game administration consisted merely of limiting the citizen's shooting privileges, there was little room for experimentation. All citizens had to be treated alike. Experiments, if any, had to be made on the state as a whole, or on all portions offering similar conditions. In other words, the technique of restriction was a legal technique which did not admit of experimental procedure. Policies had to be settled in the abstract, and then enacted into law, for better or for worse.

The new idea is different. Its central thesis is not the limitation of rights and privileges, but rather the fostering of effort. The state is just as free to experiment in better cropping methods for game as in better cropping methods for corn or pine trees. In other words the technique of production is a biological or agricultural technique; policies may be settled by concrete trial, and enacted into law, if necessary, *after* it is found whether or not they work.

But the old habit of determining policy in the abstract still persists. It must be broken down.

Our effort to settle biological questions by abstract logic is like that of the doctors who several centuries ago were arguing over the question of whether the blood circulates in the body. They banged the table long and mightily, proving to each other that it must be so, and that it couldn't be so. When they were nearly worn out, one of them had the brilliant idea of trying an experiment to find out whether it were so or not. Thereupon the argument ended, and the doctors had time to tend their patients.

The beginning and the end of this controversy illustrate the two approaches to questions of game policy: (1) the abstract, and (2) the factual or experimental.

Game managers are the doctors of our game supply. The set of ideas which served to string out the remnants of the virgin game supply, and to which many conservationists feel an intense personal loyalty, seems to have reached the limit of its effectiveness. Something new must be done. The different ideas as to what it is are not too numerous to prevent giving all of them a trial. The American Game Policy simply enumerates some of these differences, and urges that they be subjected to the test of experience.

The detail of any policy is an evanescent thing, quickly outdated by events, but the experimental approach to policy questions is a permanent thing, adaptable to new conditions as they arise. Shorn of changeable detail, it might be boiled down to these words:

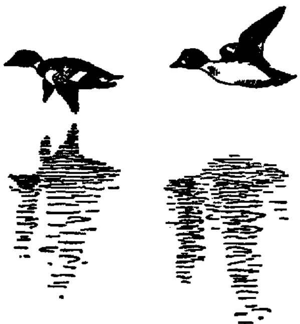
AN AMERICAN GAME POLICY

1. America has the land to raise an abundant game crop, the means to pay for it, and the love of sport to assure that successful production will be rewarded.

2. There are conflicting theories on how to bring the land, the means of payment, and the love of sport into productive relationship with each other. No one can confidently predict which theory is "best." The way to resolve differences is to bring all theories susceptible of local trial to the test of actual experience. The "best" plan is the one most nearly mutually satisfactory to the three parties at interest, namely the landowner, the sportsman, and the general public. No other plan is likely to be actually used.

3. There are some, but not enough, biological facts available on

how to make the land produce game. All factions, whatever their other differences, should unite to make available the known facts, to promote research to find the additional facts needed, and to promote training of experts qualified to apply them.



CHAPTER XVIII

GAME AS A PROFESSION

The Transition. In 1910 there were scarcely a hundred trained foresters in the country. They held only a small percentage of the positions then open. The rest were held by untrained men.

In 1930 there were over 5000 trained foresters, holding a large percentage of a much larger number of positions, in both public and private organizations. Forestry in two decades experienced a complete transition to a professional basis (Graves and Guise, 1932).

One of the most important aspects of the transition has been its effect on the pre-existing "untrained" men. Hundreds of field officers in the public service, though devoid of formal schooling, have, by contact with foresters, by personal study, and by attendance at forestry training camps, picked up a point of view, a technical understanding, and a degree of skill equal to and sometimes greater than that of their school-trained co-workers. The untrained men unable to accomplish this process of self-education have tended to drop out. The teaming of school-trained with unschooled but experienced and open-minded field workers has stimulated both.

The same transition has taken place in agricultural administration.

The same transition has now begun in the field of game. Game men in both public and private employ must become technicians, or be gradually replaced. Game management must become a profession if game conservation is to become a fact.

Personal Qualifications for Game Work. Kind and amount of schooling is of great importance to a professional career in game, but less so than the personal aptitudes of the student.

A pre-existing enthusiasm for wild life and its conservation is the first essential.

Mere enthusiasm, however, has failed to conserve game in the past, and is not likely to succeed better in the future. There is needed also a willingness and ability to know and use the intellectual tools available in varied fields of pure and applied biology. This implies two things. First, a game man, even if not engaged in research, must be by nature a scientific investigator, because the greater part of the facts he uses he must find for himself. Training cannot hope to do much more than teach him where and how to look for them. Second, a game man, even working alone in a private capacity, must be co-operative to the extent of habitually exchanging services and information. The lone worker is doomed to be overwhelmed by tasks undone, and questions unanswered.

Personal experience with land and with farm, forest, or other land crops, and with dogs and shooting, is of course of great value.

The game manager must eventually acquire what is called "the scientific point of view," but this need not pre-exist in the student. Nor should its acquisition be a matter of taking, hook-bait-and-sinker, the point of view of any academic biologist. Cloudy thinking and pottering performance are sometimes condoned in the name of scientific caution, and brilliant work may lose part of its true value by reason of academic indifference to its practical applications.

Preoccupation with rewards is a drawback. Game management uses economic forces, but for the attainment of a non-economic objective. Like most professions it yields little more than a living. Considerations of profit are not sufficient to sustain a life-long effort in its behalf.

Degrees and Kinds of Professional Training. An error was made in the early days of forestry by failing to foresee that men of various degrees and kinds of training would be required. Dozens of schools for years turned out only an intermediate degree of training, with a consequent later over-supply in this grade, and a simultaneous shortage in the higher and lower grades.

Three principal degrees of professional training are now recognized:

DEGREE OF TRAINING	KIND OF POSITION IN VIEW	PREVIOUS TRAINING REQUIRED	TOTAL YEARS POST-HIGH SCHOOL WORK TO COMPLETE	DEGREE RECEIVED
Vocational	Forest Ranger	High School	½–2	None
Technical	Forest Administration	At least 2 years undergraduate work	5–6	Master
Scientific	Forest Research	Full undergraduate course	7–8	Doctor

The same degrees of training are likewise needed in game personnel.

Vocational Training should teach skill in the performance of management work on the ground. Game management as a vocation is equivalent to "dirt-farming." Vocational courses are the equivalent of the "short course" in agriculture. They should teach what to do to the land and how to do it, but cannot hope to penetrate very deeply into the biological reasons why. Graduation from high school should be the minimum preparation for a vocational course. A 1–2 year vocational training course in one branch of game management, namely game farming, is offered at the Conservation Institute, Clinton, New Jersey.

District game wardens, estate and club superintendents, and game managers for co-operative farm groups, should ultimately be recruited from vocational schools.

Success in research or administration carries the penalty of ultimately joining the swivel-chair "overhead"; a career as a field warden, keeper, or local manager, on the other hand, stays close to the soil. As proved over and over again in forestry and agriculture and game, there is no more effective conservationist than the field man who succeeds in keeping his mind young. Facilities for mental stimulus, such as the training camps and short courses offered to field workers in forestry and agriculture, are not as yet available to the game warden, but they will come.

Technical Training should prepare men for professional work in game administration and in private practice as game experts. It should emphasize what to do and how to do it, but should also include the foundational studies necessary to understand why it is done. Among these should be a little forestry, a little agriculture, and a rather thorough grounding in game esthetics, economics, and policy. Technical training could start in the junior university year. In the opinion of the writer, no institution is as yet offering this kind of training in game.

State game wardens, game managers for large blocks of land, private practitioners in game management, technical advisors to land-using industries, and men to make game surveys should ultimately be recruited from this group.

Scientific Training should prepare men for professional research and teaching work. It should take graduate biologists and teach them how to use their biology in solving game management problems. Graduate biologists are already turned out by many universities. What needs to be developed is the second and vital step of application. The School of Forestry and Conservation at the University of Michigan has undertaken to cover this omission.

A limited number of game fellowships, financed by the Sporting Arms and Ammunition Manufacturers' Institute, were set up in 1928 to encourage universities to apply their biological manpower to game management. These unfortunately could not be renewed during the present depression. Some states and private donors, however, have begun to set up fellowships for game research, notably in Michigan and Iowa.

A scientific course in game should include a little forestry, agriculture, game esthetics, economics, and policy.

Directors of game research in universities, specialists for the U. S. Biological Survey, and teachers of game management should ultimately be recruited from this group.

Preparatory Courses. To students who think they wish to take up game work, but do not know its detailed nature, this advice is applicable: (1) Read some of the starred material in the bibliography; (2) Get a summer job with some competent practitioner.

To students who know they want to work with game, but do not know how to guide their studies to that end, advice can be less freely offered. All biological professions, including game, are ramifying into such a maze of specialized fields as make it increasingly difficult to prescribe courses. Moreover, courses carrying the same label *differ so radically in content and merit* that a list of courses means little or nothing without likewise specifying the teacher and the institution. Hence no such list can be given here. Some authoritative impartial scientific body should undertake to list and describe suggested preparatory courses for new professions such as game.

The following list of arts and sciences so far directly involved in game management may be of some service to those unfamiliar with its subject matter. No one individual, of course, ever acquires proficiency in more than a part of these subjects, but he should know enough about them to know when to consult the specialists in each, and how to interpret their advice.

SCIENCES	ARTS
Ecology	Agronomy
Ornithology	Forestry
Mammalogy	Animal Husbandry
Botany	Watersheds

SCIENCES	ARTS
Entomology	Horticulture
Herpetology	Agricultural Engineering
Parasitology	
Bacteriology	
Meteorology	
Soils and Geology	
Land Economics	
General Zoology	
Physiology	
Biometry and Statistics	

Orientation Courses. There is a distinct need for incidental orientation in game management as a preparation for professional work in forestry, agriculture, and range management. To develop an understanding of game management in the minds of county agents, teachers in agricultural high schools, and foresters is just as necessary as to develop professional game managers.

Orientation courses in game are now offered at the University of Minnesota and at several forest schools.

Choosing a Career. The choice between vocational, technical, and scientific training depends first of all on how much schooling the prospective game man is willing and able to undertake. Only those who are sure they have the mentality, inclination, and means of support for seven or eight years of hard study should seek scientific training as here defined.

The choice should depend even more, however, on the natural bent of the student. There are two kinds of game men: discoverers and organizers. The former belong in research, although even there a little organizing ability will not come amiss. The latter belong in the field of administration or technical practice, but even there an insatiable curiosity helps success. The student whose main interest in game centres on "the outdoor life," but who lacks special interest either in finding new facts or inducing people to do new things, may well pause before entering the game field at all.

The choice must depend, finally, on the prospect for openings. The number of prospective openings for trained men is certainly greatest in the vocational grade and least in the scientific grade; the initial compensation now follows the reverse order, and will presumably so continue.

There are not a few graduate students who have already decided to work in some field of biological research, but who are undecided whether to try game or something else. To such it may not be amiss to point out one respect in which game research differs from most other scientific fields: the net result of a life-time of exploration and discovery is *not* likely to be a merely economic gain to society. To him who cares what kind of mice his trap catches, this fact may prove a useful guide in the selection of a scientific doorstep.

The Rôle of Universities. The study of wild life was once a matter exclusively for ornithologists and mammalogists. It is now clear that these men cannot work alone. For really well-rounded work they require the daily help of parasitologists, bacteriologists, pathologists, botanists, entomologists, geologists, soils experts, agronomists, geneticists, meteorologists, chemists, and mathematicians. It is literally impossible to set up for game alone all of the varied personnel required for successful research. Hence the more difficult researches must be conducted where *such personnel already exists.* There are only two such places—the U. S. Department of Agriculture and the universities. Information on game can be collected by individuals anywhere, but its full interpretation ultimately requires these larger groups.

Management research is more than the study of wild life. It must also find out how to modify farming and forestry methods in favor of game. As already pointed out, these researches cannot be directly performed by game departments. They belong in the Federal Department of Agriculture, with its co-operating chain of agricultural colleges and forest schools.

These institutions already have their hands more than full. Should they *volunteer* to work out methods of game cropping? Landowners are not audibly *demanding* that they do so. It may be well to remember, however, that the job of working out improved farming methods was not thrust upon our agricultural institutions by farmer-demand. They grasped it as an opportunity, and later showed the farmers why. Neither, to my knowledge, has been sorry since.

The working equipment necessary for a university game program may be roughly classified as follows:

1. Man-power in the biological sciences.
2. Experts in the other land crops, with which the game crop must be dovetailed.

3. Field man-power, such as county agents, for extension to and education of landowners.
4. Land for demonstrations.
5. A game expert.
6. Funds.

It is clear that the first four items are found in almost any university, whereas the last two are almost always lacking at the outset. How can they be obtained?

Experience has so far disclosed six sources of funds:

1. Conservation departments.
2. Special legislative appropriations.
3. Industrial fellowships.
4. Private donors.
5. Game foundations.
6. Scientific foundations.

But money and scientific facilities are often not usable without at least one trained game manager to tie them together. To fill this need some universities have borrowed qualified men directly from the U. S. Biological Survey. The Survey also offers advisory service for specific activities such as game fellowships. Fellowships will eventually create an additional supply of game experts suitable for the guidance of university programs.

The recent appointment by the National Research Council of a committee on wild life studies is in effect a recognition of the expanding rôle of universities in this field.

Growth of Game Research. There has been a perceptible acceleration of game research in the past few years. Five years ago there were only two or three full-time workers outside the U. S. Biological Survey, which was and is, of course, the national clearing-house for such work. On July 1, 1930, the universities alone had at least 22 men, financed as follows:

By game commissions	11
By industrial fellowships	4
By universities themselves	2
Privately or by associations	5
	22

Fig. 35 shows the geographic distribution and subject matter of projects in game research and education current in 1932. In drawing the map it was necessary to follow certain arbitrary definitions of what constitutes a "project." Worthy and valuable work is under way which does not appear on the map, some because excluded by these definitions, and some doubtless because unknown to the author.

Some universities are starting to teach game management as well as to conduct game research. This is admirable, provided it be not overlooked that facts about game must be found before they can be taught. Writing curricula for game courses is as easy as pasting labels on a row of bottles, but is important only when there is something in the bottles.

It is only fair to point out, anent all these anticipated expansions in man-power and subject matter, that they are premised on an assumption which the reader should not accept simply because the author does. The assumption is this: that the conservation movement will "carry on."

There are two ways to interpret the present evidence. One is to consider the movement as merely the dying gesture of an obsolete ideal, the regretful sigh of an outdated minority as they hand over to chemists and engineers their proxy for dominion over the earth. The small proportion of young conservationists, and possibly the incessant bickerings of old ones, lend color to this view.

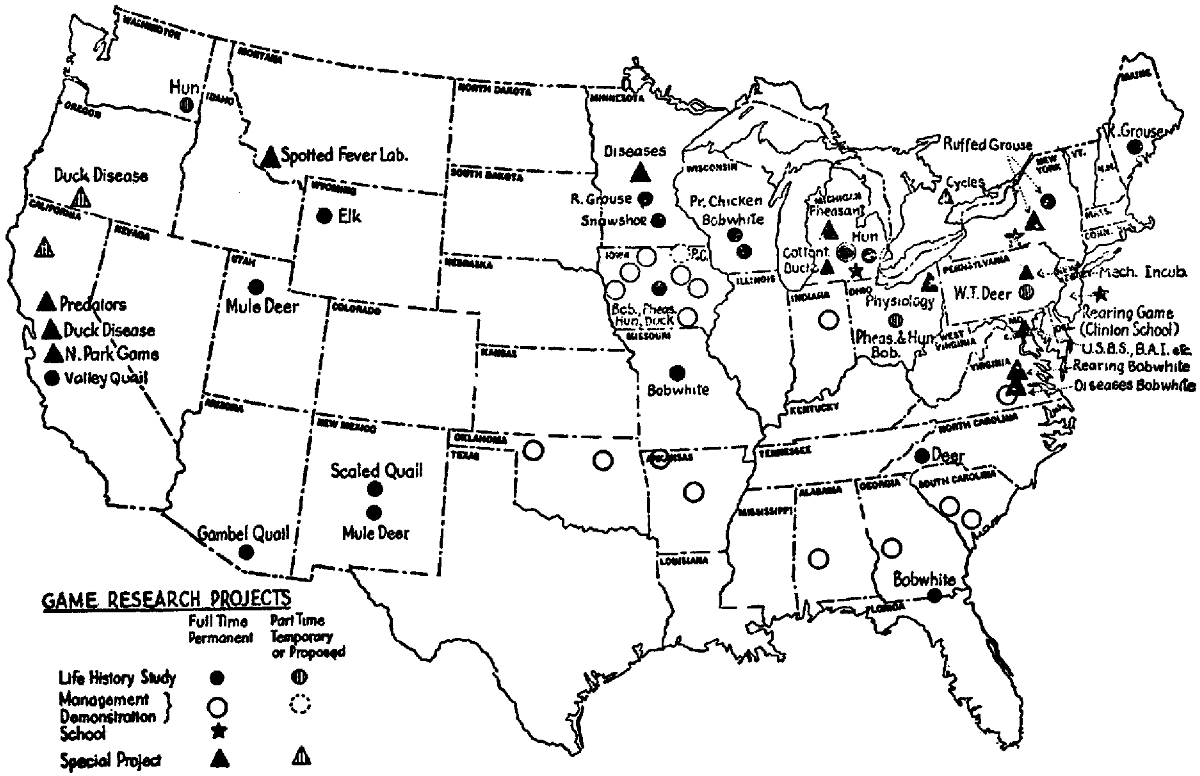
The other view is to consider the conservation idea as the beginnings of a new conviction that machines alone do not truly liberate mankind; that leisure and security are of little value if, in the process of getting them, the objects on which they could be profitably expended will have disappeared; that the task of the future is to learn how to live with our inventions.

If the first interpretation is correct, society has no future need for game managers, and the man who wants to be one may end up as an intellectual Crusoe.

Social Significance of Game Management. The game manager manipulates animals and vegetation to produce a game crop. This, however, is only a superficial indication of his social significance. What he really labors for is to bring about a new attitude toward the land.

The economic determinist regards the land as a food-factory. Though he sings "America" with patriotic gusto, he concedes any factory the right to be as ugly as need be, provided only it be efficient.

Fig. 35.



Hun
Spotted Fever Lab.
Duck Disease
Elk
Predators
Duck Disease
N. Park Game
Valley Quail
Mule Deer
Scaled Quail
Mule Deer
Gambel Quail
Diseases
R. Grouse
Snowshoe
Pr. Chicken
Bobwhite
Bob., Pheas. Hun, Duck
Bobwhite
Michigan Pheasant
Hun
Cottont. Duck
Physiology
Pheas. & Hun Bob.
Cycles
Ruffed Grouse
R. Grouse
W.T. Deer
Mech. Incub.
Rearing Game (Clinton School)
U.S.B.S., B.A.I. etc.
Rearing Bobwhite
Diseases Bobwhite
Deer
Bobwhite
GAME RESEARCH PROJECTS
Full Time Permanent
Part Time Temporary or Proposed
Life History Study
Management Demonstration
School
Special Project

There is another faction which regards economic productivity as an unpleasant necessity, to be kept, like a kitchen, out of sight. Any encroachment on the "parlor" of scenic beauty is quickly resented, sometimes in the name of conservation.

There is a third, and still smaller, minority with which game management, by its very essence, is inevitably aligned. It denies that kitchens or factories need be ugly, or farms lifeless, in order to be efficient.

That ugliness which the first faction welcomes as the inevitable concomitant of progress, and which the second regretfully accepts as a necessary compromise, the third rejects as the clumsy result of poor technique, bunglingly applied by a human community which is morally and intellectually unequal to the consequences of its own success.

These are simply three differing conceptions of man's proper relation to the fruitfulness of the earth: three different ideas of productivity. Any practical citizen can understand the first conception, and any esthete the second, but the third demands a combination of economic, esthetic, and biological competence which is somehow still scarce.

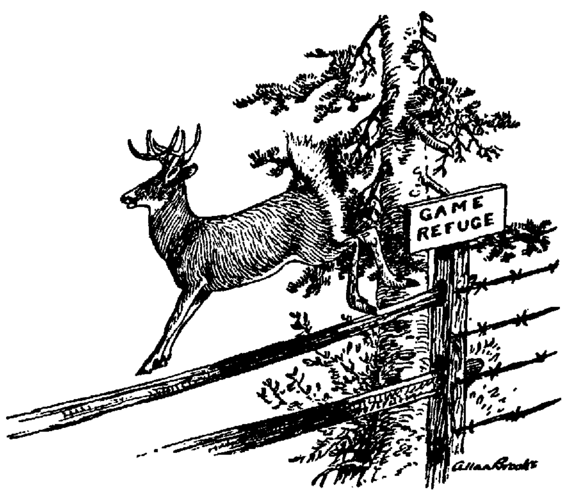
It would, of course, be absurd to say that the first two attitudes are devoid of truth. It seems to be an historical fact, however, that such few "adjustments" as they have accomplished have not kept pace with the accelerating disharmony between material progress and natural beauty. Even the noble indignation of the second school has been largely barren of any positive progress toward a worthier land-use.

Quite evidently we are confronted with a conflict of priorities —a philosophical problem of "what it is all about." Our moral leaders are so far not concerned with this issue. A few naturalists have attempted to formulate it (see Lewis, 1927; Bailey, 1915), but the conservation periodicals have been "gun-shy."

The discussion of this paradox is of course beyond the scope of this volume. I suspect, however, that the principle of factual procedure as distinguished from abstract argument, already advocated for the formulation of game policy, applies to this larger question. Examples of harmonious land-use are the need of the hour.

Herein lies the social significance of game management. It promulgates no doctrine, it simply asks for land and the chance to show that farm, forest, and wild life products can be grown on it, to the mutual advantage of each other, of the landowner, and of the public. It proposes a motivation—the love of sport—narrow enough actually to get action from human beings as now constituted, but nevertheless capable of expanding with time into that new social concept toward which conservation is groping.

In short, twenty centuries of "progress" have brought the average citizen a vote, a national anthem, a Ford, a bank account, and a high opinion of himself, but not the capacity to live in high density without befouling and denuding his environment, nor a conviction that such capacity, rather than such density, is the true test of whether he is civilized. The practice of game management may be one of the means of developing a culture which will meet this test.



APPENDIX

APPENDIX

(A) BIBLIOGRAPHY

NOTE: A relatively complete bibliography of books on sport, natural history and conservation from 1852 to 1925 is Phillips' *American Game Mammals and Birds* (1930).

Special lists of references on particular subjects are to be found in Chapters X, XI, XIII, and XV.

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(B) GLOSSARY

OF TERMS USED IN GAME MANAGEMENT

Accident. Death or injury from physical causes alone.

Administration (game). The art of governing the practice of game management.

Aftermath. Vegetation which springs up on grain stubble after the grain has been cut.

Area-kill. The annual kill per unit area.

Artificial establishment. A planting of game maintained only through renewed plantings or artificial propagation.

Bait-cover. Cover of the preceding year's growth left to attract early nests.

Band. A loose aggregation of game, sometimes all of one sex.

Beat. A European term for the territory in charge of one gamekeeper.

Blank. Part of a game range unpopulated by game.

Blow-up. A suddenly increased rate of spread in a fire.

Breeding (*or reproduction*) *potential.* The maximum or unimpeded increase rate of a species in an "ideal" environment.

Buffer. A species constituting food for predators and acting as a "buffer" to protect game from predators.

Carrying capacity. The maximum density of wild game which a particular range is capable of carrying.

Check-out system. Measuring the number of hunters or their kill by checking them in and out at points of entry and exit.

Chipped egg system. A modification of the Euston system. See Sprake.

Chipping period. The length of the interval between the first chipping or pipping of a clutch of eggs and the completion of hatching.

Clocker. A fecal pellet or dropping characteristic of incubating grouse.

Colony survival. A planting of game resulting in a small non-spreading colony.

Compound set (*or clutch*). A nest of eggs laid by more than one hen.

Covert. A geographic unit of game cover.

Covey. A small flock of birds which "lie." Syn.—bevy.

Crash. The period of severe mortality following the peak of a cycle.

Cruising radius. The distance between locations at which an individual animal is found at various hours of the day, or at various seasons, or during various years. See mobility.

Cycle. A periodic fluctuation in game density.

Density. The number of head of game per acre or other unit area carried by a game range. Syn.—stand.

Desertion limit. The number of days after incubation starts when normal disturbances of the nest will not cause desertion.

Dispersion failure. A planting of game followed by immediate dispersal and disappearance.

Driving. A form of shooting in which game is rounded up and driven past the guns.

Efflux. Game which moves out of an area. Syn.—outflow.

Escape-covert. A covert serving as refuge from predator attack, by reason of density or mechanical protection.

Euston system. Artificial incubation of eggs while the hen sets on "dummies." Incubated eggs are replaced just before pipping.

Factor. One of the forces reducing the numbers (decimating factors) or retarding the increase rate (welfare factors) of game.

Flight-limit. The maximum distance a bird can traverse at one continuous flight.

Flushing-rod. A rod attached to a mowing machine to flush incubating birds, and thus avoid cutting-over their nests.

Harassment. Interference by predators with the normal movements and actions of game.

Herd. Any large aggregation, or detached unit, of hoofed mammals.

High (noun). The peak of a cycle. A period of abundance.

Index. A condition which can be measured, and which varies as some other condition which cannot be measured. The former is used as an index to the latter.

Index plant. A plant indicating the whereabouts of game, or the suitability of a range for game.

Indicator. A condition which is visible, and which denotes some other condition which is invisible.

Influence. An environmental variable which influences a factor.

Influx. Game which moves into an area.

Interspersion. The degree to which environmental types are intermingled or interspersed on a game range.

Irruption. A large, sudden, non-periodic increase in density, often accompanied by an extension into hitherto unoccupied range.

Kill. The number of head killed per year from a unit of population.

Kill-ratio. The proportion or per cent of the game population which can be killed yearly without diminishing subsequent crops. The ratio of the yield to the population.

Leak. A loss in productivity caused by some factor.
Leakage (in drives). The game which leaks through or escapes being flushed by the line of beaters.
Limiting factor. The factor which outweighs all others in limiting productivity.
Lincoln index. A ratio based on banding and used for census.
Loafing cover. A place offering shade in summer or sun and wind protection in winter for idling.
Low (noun). The trough of a cycle. A period of scarcity.

Management (game). The art of producing sustained annual crops of wild game for recreational use.
Mobility. The tendency of the individual animal to change location during the day, or as between seasons or years. See cruising radius.

Niche. A habitable position. The place occupied by a species in relation to other species.
Normal kill. The kill sustained by the most productive unit of range or population. Syn.—normal yield.

Pack. A large compact winter flock of grouse, sometimes all of one sex.
Pastime foods. Foods eaten for pastime, rather than palatability or value.
Pellet. A mass of indigestible hair, bones, etc., regurgitated by raptorial birds or cats.
Pipping. The breaking of the eggshell by the hatching chick.
Plimsoll line. The stratum of browsed-off foliage visible in deer yards and other heavily grazed areas. Its "depth" measures the "reach" of the species in question. (The Plimsoll line of ships measures the depth to which they may be laden.)
Point of resistance. The minimum population or density necessary for recovery of productivity.
Preserve. A game-shooting ground.
Productivity. The rate at which mature breeding stock produces other mature stock, or mature removable crop.
Property. A characteristic of a game species or population.
Public shooting ground. A preserve operated by and for the public.

Recessive establishment. A planting of game followed at first by vigorous increase but later by partial decline.
Refuge. An area closed to hunting in order that its excess population may flow out and restock surrounding areas. Syn.—sanctuary.
Refuge cover. Vegetation from which game cannot be driven by hunters.

Release: kill ratio. The ratio of the number of head of game annually released for restocking, and the number killed.

Remise. A European term for an artificially established game-bird covert. Sometimes includes food as well.

Re-nesting. A nesting attempt which follows an earlier failure. (*Not* a second brood following an earlier success.)

Repeat. A second attempt to nest (see renesting). Also a second capture of a bird in the same trap where first banded.

Reproduction potential. See Breeding Potential.

Reservation. An area closed to hunting. Same as a refuge, but bearing no functional relation to its immediate surroundings.

Rest period. The period when an incubating hen normally leaves the nest for rest, food, or recreation.

Sanctuary. A refuge. Used in preference to refuge where the emphasis is on protection rather than production through outflow.

Saturation point. The maximum wild density common to widely separated optimum ranges.

"*Songbird list.*" A law listing game birds as songbirds under yearlong protection.

Squealer. A partially grown young grouse or quail. Usually refers to abnormally young birds found during the hunting season. Syn.—"cheeper."

Stand. The density or volume per acre of a crop of timber, grain, or game. Syn.—density.

Straggling failure. A planting of game followed by initial thrift but ultimate dwindling and disappearance.

Street. A line of cover connecting coverts or feeding grounds, and serving as an avenue of travel.

Success ratio. The ratio of number of hunters to number of game killed.

Succulence. Food of high moisture content.

Toll. A charge for hunting privileges by the day or by the head.

Yard. A wintering ground used by deer during deep snow. Paths are trampled down to afford access to browse food.

Yield. The sustained kill per unit of area or population.

Yield table. A table showing the annual kill per unit area for various population densities, or for various site qualities, in blocks of various size.

(C) BREEDING POTENTIAL TABLES

UNIMPEDED INCREASE RATE OF POPULATIONS

(Starts with one adult pair. Assumes sex ratio 50:50. Disregards longevity but all progressions stop at 30 yrs. or 5000 population. Figures as of Jan. 1)

SPECIES BEARING FIRST YOUNG AT I YEAR

Year	Number of Young Per Year																
	1	2	3	4	5	6	7	8	9	10	12	13	14	15	16	18	20
1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
2	3	4	5	6	7	8	9	10	11	12	14	15	16	17	18	20	22
3	4	8	11	18	22	32	37	50	56	72	98	106	128	137	162	200	242
4	6	16	26	54	77	128	163	250	308	432	686	795	1024	1157	1458	2000	2662
5	9	32	65	162	267	512	730	1250	1694	2592	4802	5956	8192	9827	11664	20000	29282
6	13	64	161	486	932	2048	3285	6250	9317	15552	33614						
7	19	128	401	1458	3012	8192	14779										
8	28	256	1001	4374	10542												
9	42	512	2501	13122													
10	63	1024	6251														
11	94	2048															
12	141	4096															
13	211	8192															
14	316																
15	474																
16	711																
17	1066																
18	1599																
19	2398																
20	3597																
[illegible]	5395																

SPECIES BEARING FIRST YOUNG AT 2 YEARS

Year	Number of Young Per Year											
	1.0				1.5				2.0			
	Tot. =	yg +	yrlg +	ad.	Tot. =	yg	+ yrlg	+ ad.	Tot. =	yg	+ yrlg	+ ad.
1	2	0	0	2	2	0	0	2	2	0	0	2
2	3	1	0	2	3	1	0	2	4	2	0	2
3	4	1	1	2	4	1	1	2	6	2	2	2
4	5	1	1	3	5	1	1	3	10	4	2	4
5	7	2	1	4	8	3	1	4	16	6	4	6
6	9	2	2	5	11	3	3	5	26	10	6	10
7	12	3	2	7	17	6	3	8	42	16	10	16
8	16	4	3	9	24	7	6	11	68	26	16	26
9	22	6	4	12	36	12	7	17	110	42	26	42
10	30	8	6	16	54	18	12	24	178	68	42	68
11	41	11	8	22	81	27	18	36	288	110	68	110
12	56	15	11	30	121	40	27	54	466	178	110	178
13	76	20	15	41	181	60	40	81	754	288	178	288
14	104	28	20	56	271	90	60	121	1220	466	288	466
15	142	38	28	76	406	135	90	181	1974	754	466	754
16	194	52	38	104	608	202	135	271	3194	1220	754	1220
17	265	71	52	142	912	304	202	406	5168	1974	1220	1974
18	362	97	71	194	1368	456	304	608				
19	494	132	97	265	2052	684	456	912				
20	675	181	132	362	3078	1026	684	1368				
21	922	247	181	494	4617	1539	1026	2052				
22	1259	337	247	675	6925	2308	1539	3078				
23	1720	461	337	922								
24	2349	629	461	1259								
25	3209	860	629	1720								
26	4383	1174	860	2349								
27	5987	1604	1174	3209								

Year	Number of Young Per Year																							
	3.0				4.0				6.0				8.0				10.0				12.0			
	Tot. =	yg	+ yrlg	+ ad.	Tot. =	yg	+ yrlg	+ ad.	Tot. =	yg	+ yrlg	+ ad.	Tot. =	yg	+ yrlg	+ ad.	Tot. =	yg	+ yrlg	+ ad.	Tot. =	yg	+ yrlg	+ ad.
1	2	0	0	2	2	0	0	2	2	0	0	2	2	0	0	2	2	0	0	2	2	0	0	2
2	5	3	0	2	6	4	0	2	8	6	0	2	10	8	0	2	12	10	0	2	14	12	0	2
3	7	3	3	2	10	4	4	2	14	6	6	2	18	8	8	2	22	10	10	2	26	12	12	2
4	14	6	3	5	22	12	4	6	38	24	6	8	58	40	8	10	82	60	10	12	110	84	12	14
5	26	12	6	8	42	20	12	10	80	42	24	14	130	72	40	18	192	110	60	22	266	156	84	26
6	47	21	12	14	86	44	20	22	194	114	42	38	362	232	72	58	602	410	110	82	926	660	156	110
7	86	39	21	26	170	84	44	42	434	240	114	80	882	520	232	130	1562	960	410	192	2522	1596	660	266
8	155	69	39	47	342	172	84	86	1016	582	240	194	2330	1448	520	362	4572	3010	960	602	8078	5556	1596	926
9	284	129	69	86	682	340	172	170	2318	1302	582	434	5858	3528	1448	882	12582	7810	3010	1562				
10	515	231	129	155	1366	684	340	342	5366	3048	1302	1016												
11	943	426	231	284	2730	1364	684	682																
12	1712	771	426	515	5462	2732	1364	1366																
13	3122	1410	771	943																				
14	5690	2568	1410	1712																				

SPECIES BEARING FIRST YOUNG AT 3 YEARS

Year	Number of Young Per Year																			
	1.0					1.5					2.0					5.0				
	Tot.=	yg.	+ yr.	+ 2 yrs.	+ ad.	Tot.=	yg	+ yr.	+ 2 yrs.	+ ad.	Tot.=	yg	+ yr.	+ 2 yrs.	+ ad.	Tot.=	yg	+ yr.	+ 2 yrs.	+ ad.
1	2	0	0	0	2	2	0	0	0	2	2	0	0	0	2	2	0	0	0	2
2	3	1	0	0	2	3	1	0	0	2	4	2	0	0	2	7	5	0	0	2
3	4	1	1	0	2	4	1	1	0	2	6	2	2	0	2	12	5	5	0	2
4	5	1	1	1	2	5	1	1	1	2	8	2	2	2	2	17	5	5	5	2
5	6	1	1	1	3	6	1	1	1	3	12	4	2	2	4	32	15	5	5	7
6	8	2	1	1	4	8	3	1	1	4	18	6	4	2	6	62	30	15	5	12
7	10	2	2	1	5	12	3	3	1	5	26	8	6	4	8	102	40	30	15	17
8	13	3	2	2	6	16	4	3	3	6	38	12	8	6	12	182	80	40	30	32
9	17	4	3	2	8	22	6	4	3	9	56	18	12	8	18	337	155	80	40	62
10	22	5	4	3	10	31	9	6	4	12	82	26	18	12	26	592	255	155	80	102
11	28	6	5	4	13	43	12	9	6	16	120	38	26	18	38	1047	455	255	155	182
12	36	8	6	5	17	59	16	12	9	22	176	56	38	26	56	1887	840	455	255	337
13	47	11	8	6	22	81	22	16	12	31	258	82	56	38	82	3367	1480	840	455	592
14	61	14	11	8	28	112	31	22	16	43	378	120	82	56	120	5982	2615	1480	840	1047
15	79	18	14	11	36	155	43	31	22	59	554	176	120	82	176					
16	102	23	18	14	47	215	60	43	31	81	812	258	176	120	258					
17	132	30	23	18	61	299	84	60	43	112	1190	378	258	176	378					
18	171	39	30	23	79	414	115	84	60	155	1744	554	378	258	554					
19	222	51	39	30	102	574	160	115	84	215	2556	812	554	378	812					
20	288	66	51	39	132	797	223	160	115	299	3746	1190	812	554	1190					
21	373	85	66	51	171	1107	310	223	160	414	5490	1744	1190	812	1744					
22	484	111	85	66	222	1537	430	310	223	574										
23	628	144	111	85	288	2134	597	430	310	797										
24	814	186	144	111	373	3071	837	597	430	1107										
25	1056	242	186	144	484	4123	1152	837	597	1537										
26	1370	314	242	186	628	5712	1600	1152	837	2134										
27	1777	407	314	242	814															
28	2305	528	407	314	1056															
29	2990	685	528	407	1370															
30	3878	888	685	528	1777															

SPECIES BEARING FIRST YOUNG AT 4 YEARS

Year	Number of Young Per Year											
	1						2					
	Tot.=	yg	+yr.	+2 yr.	+3 yr.	+ad.	Tot.=	yg	+yr.	+2 yr.	+ 3 yr.	+ad.
1	2	0	0	0	0	2	2	0	0	0	0	2
2	3	1	0	0	0	2	4	2	0	0	0	2
3	4	1	1	0	0	2	6	2	2	0	0	2
4	5	1	1	1	0	2	8	2	2	2	0	2
5	6	1	1	1	1	2	10	2	2	2	2	2
6	7	1	1	1	1	3	14	4	2	2	2	4
7	9	2	1	1	1	4	20	6	4	2	2	6
8	11	2	2	1	1	5	28	8	6	4	2	8
9	14	3	2	2	1	6	38	10	8	6	4	10
10	17	3	3	2	2	7	52	14	10	8	6	14
11	21	4	3	3	2	9	72	20	14	10	8	20
12	26	5	4	3	3	11	100	28	20	14	10	28
13	33	7	5	4	3	14	138	38	28	20	14	38
14	41	8	7	5	4	17	190	52	38	28	20	52
15	51	10	8	7	5	21	262	72	52	38	28	72
16	64	13	10	8	7	26	362	100	72	52	38	100
17	80	16	13	10	8	33	500	138	100	72	52	138
18	100	20	16	13	10	41	690	190	138	100	72	190
19	125	25	20	16	13	51	952	262	190	138	100	262
20	157	32	25	20	16	64	1314	362	262	190	138	262
21	197	40	32	25	20	80	1814	500	362	262	190	500
22	247	50	40	32	25	100	2504	690	500	362	262	690
23	309	62	50	40	32	125	3456	952	690	500	362	952
24	387	78	62	50	40	157	4770	1314	952	690	500	1314
25	485	98	78	62	50	197	6584	1814	1314	952	690	1814
26	608	123	98	78	62	247						
27	762	154	123	98	78	309						
28	955	193	154	123	98	387						
29	1197	242	193	154	123	485						
30	1501	304	242	193	154	608						

(D) INDEX

Note: Authors cited in text and bibliography are capitalized. Cases are indexed by (1) subject matter, (2) species, (3) state. If the reader fails to find any given matter under one category, he should try the other two. Pages refer to maps and tables, as well as text references. Latin names are omitted except when common names are lacking.

GAME MANAGEMENT

ALDO LEOPOLD

With this book, published more than a half-century ago, Aldo Leopold created the discipline of wildlife management. For more than forty years it was the leading textbook in the field, and today it still offers a perspective lacking in modern texts.

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