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Captive breeding genetics and reintroduction success

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ABSTRACT

Since threatened species are generally incapable of surviving in their current, altered natural environments, many conservation programs require to preserve them through ex situ conservation techniques prior to their reintroduction into the wild. Captive breeding provides species with a benign and stable environment but has the side effect to induce significant evolutionary changes in ways that compromise fitness in natural environments. I developed a model integrating both demographic and genetic processes to simulate a captive-wild population system. The model was used to examine the effect of the relaxation of selection in captivity on the viability of the reintroduced population, in interaction with the reintroduction method and various species characteristics. Results indicate that the duration of the reintroduction project (i.e., time from the foundation of the captive population to the last release event) is the most important determinant of reintroduction success. Success is generally maximized for intermediate project duration allowing to release a sufficient number of individuals, while maintaining the number of generations of relaxed selection to an acceptable level. In cases where a long residence time in captivity cannot be avoided, the use of distinct, genetically independent captive breeding units allows more efficient purging of the genetic load in the reintroduced population, and substantially improves its viability. Overall, the study allows to identify situations in which the genetic cost associated with selection relaxation may overwhelm the demographic benefits of programs.

1. Introduction

The reintroduction of plants and animals to the wild is an important technique to save endangered species from extinction (Armstrong and Seddon, 2008). Since rare species are generally incapable of surviving in their current, altered natural environments, many conservation programs are required to preserve them through ex situ conservation techniques (captive breeding, zoos, aquaria, arboreta, gene and seed banks) before the reintroduction phase can be achieved. The success of reintroduction programs is difficult to assess because such assessment requires long term data as well as general and accepted success criteria, which are both lacking. In most empirical surveys on reintroductions, programs are considered successful if they result in self-sustaining populations (Griffith et al., 1989; Fischer and Lindenmayer, 2000). While failures are easy to identify in some cases (e.g., when extinction is documented), the assessment of successes may require the use of various criteria (survival or fecundity rates, population trend, spatial expansion...) to determine whether or not the population is self-sustaining. Because reintroduced populations are generally small and may exhibit a demographic disequilibrium (e.g., in terms of sex or age structure) affecting their short-term dynamics, it is important to assess their viability after a sufficiently long time. This can be achieved easily with population dynamics models, which allow computing and comparing long-term extinction rates for various situations or release methods. For animal species, general empirical surveys on reintroduction success have concluded that success is generally low (38%, Griffith et al., 1989; 11%, Beck et al., 1994) and that reintroduction projects using captive-bred animals were significantly less successful than those using wild animals (Griffith et al., 1989; Wolf et al., 1996; Fischer and Lindenmayer, 2000; Jule et al., 2008).

Ex situ techniques provide species with a benign and stable environment (through e.g., food supplementation, health care, reduction of parasite and disease loads, removal of predators) in order to ensure high and temporally stable population growth and high probability of long term persistence. Although captivity may cause physiological, behavioral or ecological problems, empirical results in various species indicate that fecundity and survival rates are generally higher in captive than in wild populations (e.g., Ricklefs and Scheurlein, 2001). In Salmonids, for instance, survival from egg to smolt stages is typically 85–95% in hatcheries but only 1–5% in the wild (Reisenbichler et al., 2004).

The cost of this demographic security is that captive populations may undergo significant evolutionary changes in ways that compromise fitness in natural, non benign environments (Ruzzante and Doyle, 1993). There are many empirically documented

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examples of reductions in fitness caused by captive propagation (Fleming et al., 1996; Bryant and Reed, 1999; Lomnicki and Jasienski, 2000) and recent results indicate that the reduction of reproductive capabilities in the wild can be as fast and as strong as 40% decline per captive-reared generation (Araki et al., 2007).

Depending on the captive conditions, populations may face different types of genetic problems in captivity: (i) a high level of inbreeding due to small population size, and the resulting reduction of fitness due to inbreeding depression (Ralls et al., 1988); (ii) the progressive fixation and accumulation of mildly deleterious mutations through genetic drift (Bryant and Reed, 1999); (iii) the loss of genetic diversity (Neveu et al., 1998), (iv) genetic adaptations to captivity that are deleterious in the wild (Frankham, 2008). Importantly, these different problems may be either associated with small population size, captive benign conditions, artificial selection, or their interactions.

As a consequence of this variety of ecological and evolutionary processes, optimal management strategies for restored populations are dependent on the goal and focus of the programs. First, management strategies that are optimal for the wild population may be the ones that are the most detrimental to the captive one, for demographic (Bustamante, 1996) and genetic (Earnhardt, 1999) reasons. Second, in the captive population, there may be genetic trade-offs among breeding strategies (e.g., strategies aiming at maximizing the genetic diversity of the captive populations by equalization of individual contributions may enhance selection relaxation (but see Rodriguez-Ramilo et al., 2006)). Third, strategies that are demographically optimal may be the ones that are likely to be the most genetically deleterious (Lynch and O'Hely, 2001).

Theoretical modeling work on the optimal management of captive-wild population systems has shown contrasting results, which reflect the diversity of evolutionary and ecological processes involved, as well as their antagonisms. From a purely demographic view-point (i.e., in the absence of genetic considerations), modeling work has shown that the best strategy to ensure species persistence is to capture the entire wild population whenever it is below a threshold of 20 individuals, provided that captive populations have better growth rates than wild populations (Tenhumberg et al., 2004). On the other hand, theoretical work on the question of relaxed selection or adaptation from captivity demonstrated negative genetic consequences of supplementation programs on the long term fitness of wild populations (Lynch and O'Hely, 2001; Ford, 2002), whereas other work pointed out the beneficial short term genetic effects of moderate gene flows (Theodorou and Couvet, 2004).

Although these theoretical studies have provided great insights to the understanding of the captive-wild population systems, their discrepancies complicate the definition of general management strategies. Besides, no theoretical genetic study has addressed the case of several independent captive breeding units, and all models cited above have been applied to the case of supplementation of existing wild populations. Despite the numerous demographic and genetic peculiarities of reintroduced populations (Robert et al., 2007) and the urgent need to develop an integrated framework to reintroduction biology (Sarrazin and Barbault, 1996; Seddon et al., 2007), few modeling studies have so far addressed the effects of genetic deterioration in species reintroductions.

The aim of the present study is to examine the effect of genetic deterioration on the dynamics and viability of populations reintroduced from captive breeding programs. It was motivated by (i) the necessity of considering practical constraints in reintroduction models; (ii) the need to integrate demographic and genetic aspects when comparing reintroduction strategies. I developed a stochastic model that explicitly described the captive and reintroduced population dynamics. The dynamics of deleterious mutations in these populations were considered, assuming that selection against deleterious alleles was relaxed in captivity. Projected long-term extinction probabilities were computed as an index of reintroduction success.

2. Methods

I used a two-sex individual-based model with overlapping generations and a yearly time step to describe the dynamics of a system of captive (one or several breeding units) and reintroduced (single, initially empty site) populations. These two components are hereafter referred to as the *captive* and the *wild* populations.

2.1. Life cycle and dynamics of the wild population

In each year t, adult males and females paired randomly according to a monogamous mating system. The female fecundity was $F(t)$ (Poisson process) and the sex of each individual was randomly determined according to a 1:1 sex-ratio. Each survival event was drawn from a Bernoulli function, with age-specific survival rates. Because the type of density dependence had little effect on extinction rates for the questions investigated and at the time scale considered, population size was simply truncated to the population's carrying capacity K_{wild} in each year. Truncation was made independently of the genetic qualities of individuals in order to keep constant selection coefficients. For simplicity, I assumed that environmental stochasticity caused inter-annual variations in fecundity, but not in survival. In each year t, the value of $F(t)$ was drawn from a Normal distribution (F, σ_F). The theoretical set of demographic parameters used in the main simulation corresponds to typical short-lived birds or mammals, with low annual adult survival rates ($s_{ad} < 0.7$) and high annual fecundity rates ($F > 4$) (parameters used are presented in Table 1). However, to examine the generality of the conclusions, I investigated other types of life cycles (corresponding, in particular, to long-lived vertebrates). The demographic parameters used for these analyses were computed with a deterministic matrix model (Legendre and Clobert, 1995) to obtain (i) different life cycles with the same generation length and different *annual* deterministic growth rates; (ii) different life cycles with different generation lengths and similar *per generation* growth rates (see empirical justification in Niel and Lebreton, 2005). These parameters are presented in Supplementary Appendix S1.

2.2. Genetic characteristics (wild population)

Genetic factors were parameterized using values from a broad array of empirical studies (Haag-Liautard et al., 2007). Empirical data indicate that mutation rates in higher eukaryotes are roughly 0.1–100 per genome per sexual generation (Drake et al., 1998) and that the distribution of mutation effects is approximately exponen-

Table 1
Set of genetic and demographic (short-lived life cycle, annual rates) parameters used for the reintroduced population in the main simulation model.

Parameter	Notation	Value
Juvenile survival rate	s_0	0.3
Adult survival rate	s_{1+}	0.55
Mean female fecundity	F	4.25
Age at maturity	a_m	1
Inter-annual variation in female fecundity	σ_F	1.0
Zygotic mutation rate (mildly delet. mutations)	U_d	1.0
Zygotic mutation rate (lethal mutations)	U_l	0.05
Coeff. of selection (mildly delet. mutations)	s_d	0.02
Coeff. of selection (lethal mutations)	s_l	1.0
Coeff. of dominance (mildly delet. mutations)	h_d	0.35
Coeff. of dominance (lethal mutations)	h_l	0.02

tial (Mackay et al., 1992). Following a widely accepted dichotomy (Wang et al., 1998), I considered two types of deleterious mutations: mildly deleterious mutations with high probability of occurrence and lethal mutations with low probability of occurrence. The genome of each individual was explicitly represented as two series of $L = 1000$ different diploid loci. Each of these series could carry two types of alleles at each locus: a wild-type and a deleterious allele. The first and second series were used to model, respectively, mildly deleterious and lethal mutations. I selected the number of loci large enough to allow the segregation and accumulation of numerous detrimental mutations within the period considered without saturating the genome. The coefficients of selection, coefficients of dominance, and average numbers of genomic mutations per generation were, respectively, $s_d = 0.02$, $h_d = 0.35$, $U_d = 1$ for mildly deleterious mutations and $s_l = 1.0$, $h_l = 0.02$, $U_l = 0.05$ for lethal mutations (Table 1). These values were used in all figures, except where the effect of mutation parameters was explicitly examined. Mean initial numbers of mildly deleterious and lethal alleles q_{0d} and q_{0l} were given by the mutation–selection balance and binomially distributed (see Falconer and Mackay, 1996).

During fertilization, the probability of transmission of each allele at each locus was given by Mendelian rules. New deleterious mutations stochastically occurred in each zygote (Poisson distributed, with means U_d and U_l). I assumed multiplicative interactions for fitness (no epistasis) and free recombination of all loci (no linkage).

I assumed that deleterious alleles acted by reducing juvenile survivorship only. The survival rate of the individual i was then given by

$$S_{0i} = s_0 \cdot w_{di} \cdot w_{li}$$

with the relative reductions in juvenile survival due to mildly deleterious and lethal alleles in individual i being given by

$$w_{di} = (1 - h_d \cdot s_d)^{nd1i} \cdot (1 - s_d)^{nd2i} \cdot w_{d0}^{-1} \quad \text{and}$$
$$w_{li} = (1 - h_l \cdot s_l)^{nl1i} \quad (1 - s_l)^{nl2i} \quad w_{l0}^{-1}$$

s_0 was the expected survival rate of mutation free individuals; $nd1i$ and $nd2i$ were, respectively, the numbers of heterozygous and homozygous mildly deleterious mutations carried by the individual i; $nl1i$ and $nl2i$ were, respectively, the numbers of heterozygous and homozygous lethal mutations carried by the individual i, and w_{d0} and w_{l0} were the expected initial reductions in survival due to mildly deleterious and lethal alleles present at time zero, given by

$$w_{d0} = (1 - h_d.s_d)^{2L.q0d} \quad \text{and} \quad w_d0 = (1 - h_l.s_l)^{2L \cdot q0l}$$

with L being the number of loci.

2.3. Captive population and translocations

Demographic and genetic processes were basically the same in the wild and captive populations. However, I assumed that (i) demographic rates were improved in captivity as compared to the wild population; (ii) selection was relaxed in captivity; (iii) there was no environmental stochasticity in the captive population; (iv) the carrying capacity of the captive population was K_{capt} (as for the wild population, regulation occurred through random truncation).

The demographic rates of the captive population were computed using γ_{dem}, which represented the proportion of improvement of fecundity and reduction in mortality in the captive environment, as compared to the wild environment. In captivity, the annual fecundity rate F' and the survival rate $s_{(x)}{}'$ between age x and $x + 1$ were, respectively, computed as

$$F' = \gamma_{dem} F \quad \text{and} \quad s_{(x)}{}' = 1 - \gamma_{dem}^{-1}(1 - s_{(x)})$$

where F was the fecundity in the wild and $s_{(x)}$ was the corresponding age-specific survival rate in the wild.

Mutation, fertilization and selection processes occurred as in the wild population, but assuming different selection parameters. I considered some relaxation of selection, assuming however that the effect of severe disorders (i.e., homozygous lethal mutations) could not be removed by any manipulation in the captive environment (see Ralls et al., 2000). Selection was then relaxed for mildly deleterious mutations (for both heterozygous and homozygous mutations) and for lethal mutations (for heterozygous mutations only).

The coefficient γ_{sel} quantified the level of selection relaxation, according to

$$S'_d = (1 - \gamma_{sel}) s_d \quad \text{and} \quad h'_l = (1 - \gamma_{sel}) h_l$$

where $s_d{}'$ and $h_l{}'$ were, respectively, the coefficient of selection of mildly deleterious mutations and the coefficient of dominance of lethal mutations in captivity.

At time zero, there was no wild population, and N_{found} individuals were initialized in the captive population (founders). This founding population constituted of adult individuals, at the mutation–selection equilibrium, with a balanced, stochastic sex-ratio. Then, in each year, a proportion R_r of captive newborns was released to the wild (Binomial process). Releases ended after the year D (duration of the reintroduction project, in years) and the remaining captive population was eliminated.

In the cases where I considered several distinct captive units, translocation from captivity to the wild occurred as for the single unit case (so that the reintroduced population was a cross among breeding units), and translocations among captive units (newborn individuals) occurred at a rate m in each year (Bernoulli process), with all units being equally connected.

2.4. Parameters investigated and simulation protocol

I was especially interested in examining the effect of program duration (D) on population dynamics, viability, and fitness evolution in the wild population. This effect was investigated in relation with other manageable parameters or reintroduction program constraints (such as N_{found}, R_r, K_{wild}, K_{capt}, γ_{dem}, γ_{sel}), and for different species life cycles. Changes in demographic and genetic properties were investigated using Monte Carlo simulations in which 2500 population trajectories were drawn over a fixed time horizon (200–500 years).

3. Results

3.1. One captive population

As a first step, the number of released individuals, and the relative fitness, dynamics and viability of the reintroduced populations were examined for various durations of the captive breeding program (D, ranging from 1 to 50 years in the main simulations) (Figs. 1–3). All results indicated that (i) the number of released individuals increased almost linearly with D; (ii) in the absence of genetic considerations, short and long-term extinction probabilities were negatively correlated with D; (iii) in the presence of genetic considerations, the fitness of the wild population decreased with increasing D.

These temporal changes in fitness, population size and viability are illustrated on Supplementary Fig. S1, while the overall effect of D on long term viability is summarized on Fig. 1a. Results indicate that viability is maximized for intermediate values of D when mildly deleterious mutations are considered. Interestingly, this effect becomes apparent only if viability is assessed after a sufficient time. In all analyses, the optimal program duration decreased with the time horizon considered for viability assessment (Fig. 1b).

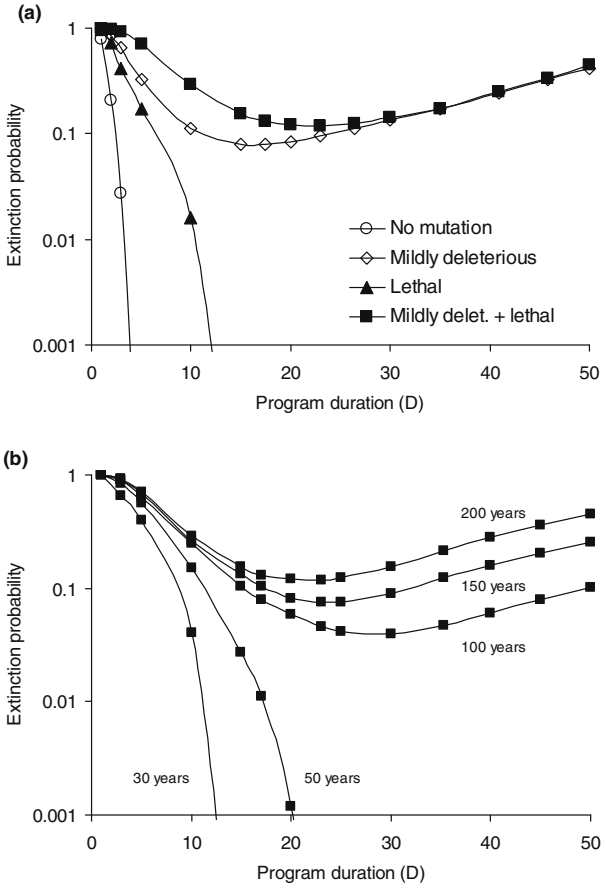

Fig. 1. Projected wild population viability as a function of the duration of the reintroduction program (D, in years). Demographic and genetic parameters are presented in Table 1. N_{found} = 20; K_{capt} = 50; K_{wild} = 500; R_r = 0.3; γ_{sel} = 1; γ_{dem} = 2. (a) Viability computed after 200 years, for different types of selected genetic variation. (b) Viability computed for different time horizons. Both mildly deleterious and lethal mutations are considered.

Although a transient genetic load due to highly recessive, lethal alleles was observed in all cases (see, e.g., Kirkpatrick and Jarne, 2000 and Supplementary Fig. S1), lethal mutations contributed little to extinction rates as compared to mildly deleterious mutations, unless the number of released individuals was small (which implied values of D comprised between 1 and 5 years). In all subsequent results, both types of mutations are considered, but the discussion is focused on mildly deleterious mutations, which contribute the most to extinction.

Sensitivity analyses indicated that the pattern observed (i.e., maximum viability obtained for intermediate D) remains qualitatively true for a broad range of parameters regarding the constraints of the reintroduction project (N_{found}, R_r, K_{wild}, K_{capt}, Fig. 2). Long term population viability logically increases with the number of founders of the captive population (N_{found}), the carrying capacity of the wild population (K_{wild}) and the rate of release (R_r), except in cases where R_r is so high that it leads to the extinction of the captive population (not shown). However, these three parameters have a modest or no effect on the value of D that maximizes wild population viability. The analysis showed that the persistence of the reintroduced population and optimal program duration are especially sensitive to the carrying capacity of the captive population (K_{capt}). As expected, reintroduction success generally increases with K_{capt} (Fig. 2c). However, if both D and K_{capt} are important, the viability of the reintroduced population may be dramatically reduced (which implies that, all other parameters being constant, an intermediate value of K_{capt} maximizes viability).

When comparing life cycles with different deterministic growth rates (λ) and generation lengths (T), no particular effect of λ was revealed (viability always increased with λ, but no effect on the optimal program duration was observed, see Supplementary Fig. S2), while T was positively related to the optimal program duration (Fig. 3). However, interestingly, the optimal duration remained approximately constant in terms of number of generations. When using results presented in Fig. 3 (where viability was computed over a 500 year time horizon for easier comparison among life cycles), the relationship between the optimal duration (in years) and the generation length was approximately linear (R^2 = 0.98). Using different life cycles (Supplementary Appendix 1), values of D minimizing the 500 year extinction probabilities ranged between 9.2 and 15 generations, while durations minimizing the 200 year extinction probabilities ranged between 12.4 and 17 generations. Thus, although the optimal duration may vary with a number of species and environmental parameters, results suggest that it represents a relatively small number of generations (10–20) for most species. Further sensitivity analysis (Supplementary Fig. S2) indicated that the qualitative conclusions presented remain true for a broad range of assumptions as long as selection is substantially relaxed in the captive population ($\gamma_{sel} > 0.5$).

3.2. Several captive populations

Comparison between one and several independent (m = 0.0) captive units (with equal total number of founders and total carrying capacity of the captive population in all cases) revealed and quantified three important processes. First, from a demographic view-point (i.e., in the absence of genetic considerations), population growth was more rapid with the single captive unit strategy, with subsequently more released individuals, and reduced extinction rates of the wild population, as compared to the several unit strategy. Second, when selection was not completely relaxed in captivity, the genetic load increased more rapidly in captive populations with several units as compared to the single-unit strategy (mildly deleterious mutations), which secondarily enhanced the demographic effect described above. Third, after the end of the release phase, rapid fitness recovery occurred in the wild population (mildly deleterious mutations). However, this recovery was much more important with the several unit strategy as compared to the single-unit strategy. Similarly, when comparing systems with several captive units with different rates of exchange among units, fitness recovery of the wild population was more important for captive units with low rates of exchange (Supplementary Fig. S3).

As a consequence of these differences in selection and fitness changes, if program duration is short, strategies involving various numbers of independent units lead to similar viability (except if the number of units is very large). However, if D is large (>30 years with the life cycle used in the main simulation), the success of the reintroduction program increases with the number of independent units (Fig. 4a). Similarly, when considering several captive units, long term viability decreases with an increasing rate of exchange among captive units (Fig. 4b). This result is robust to a wide range of conditions, as long as the level of selection relaxation is large ($\gamma_{sel} > 0.5$). If $\gamma_{sel} < 0.5$, the effect of m becomes less important and depends on particular genetic and demographic parameters (not shown).

4. Discussion

4.1. The demography–genetics trade-off

Among the number of complex dilemma faced by conservationists and managers of reintroduction programs, the demography–genetics trade-off is of major importance. On the one hand, species

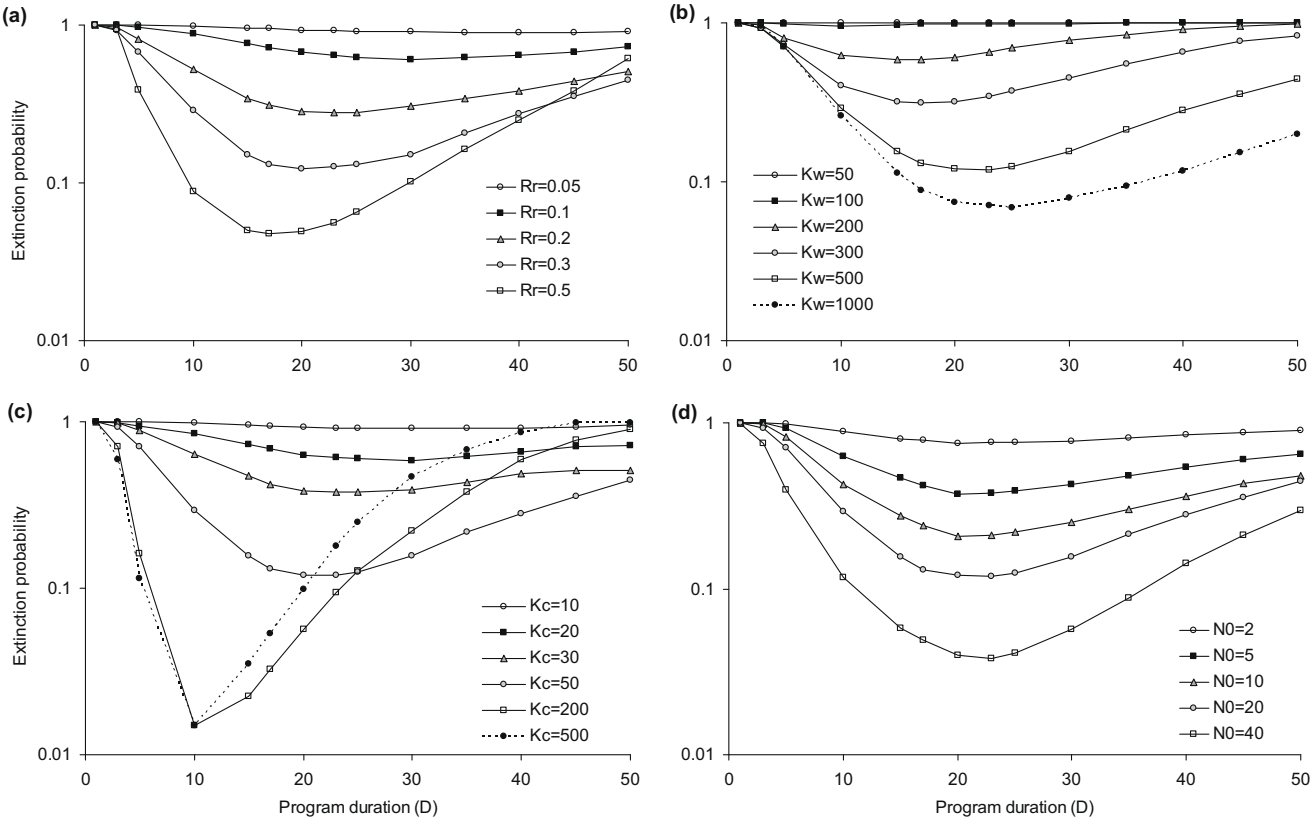

Fig. 2. Projected wild population viability (200 years) as a function of the duration of the reintroduction program (D, in years), for different values of management parameters. Demographic and genetic parameters are presented in Table 1. $\gamma_{sel} = 1$; $\gamma_{dem} = 2$. (a) Effect of the rate of release Rr, with $N_{found} = 20$; $K_{capt} = 50$; $K_{wild} = 500$. (b) Effect of the carrying capacity of the wild population K_{wild}, with $N_{found} = 20$; $K_{capt} = 50$; $R_r = 0.3$. (c) Effect of the carrying capacity of the captive population K_{capt}, with $N_{found} = 20$; $K_{wild} = 500$; $R_r = 0.3$. (d) Effect of the number of founders of the captive population N_{found}, with $K_{capt} = 50$; $K_{wild} = 500$; $R_r = 0.3$.

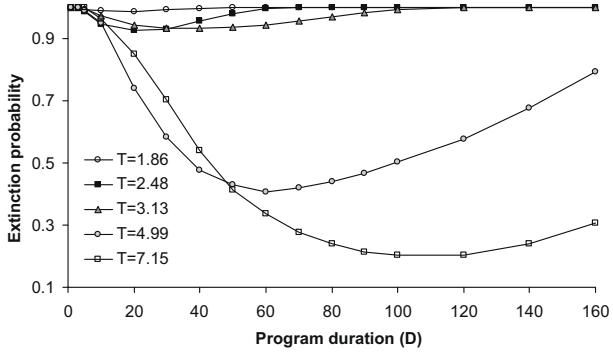

Fig. 3. Projected wild population viability (500 years) as a function of the duration of the reintroduction program (D, in years), for species with different generation lengths. Genetic parameters are presented in Table 1. Demographic parameters were computed to obtain different generation times and equivalent per generation growth rates (details presented in Supplementary Appendix 1). $N_{found} = 20$; $K_{capt} = 50$; $K_{wild} = 500$; $R_r = 0.3$; $\gamma_{sel} = 1$; $\gamma_{dem} = 2$.

that have spent several generations in captivity may have undergone important and deleterious evolutionary changes, due to the accumulation of mutations that are deleterious in the natural but not in the captive environment (Bryant and Reed, 1999; McPhee, 2003). The present results show indeed that such changes may lead to important reduction of fitness in the wild and subsequent high extinction risk, in qualitative agreement with previous modeling studies focusing on the dynamics of deleterious mutations (Lynch and O'Hely, 2001), or using quantitative genetic models under local stabilizing selection (Tufto, 2001; Ford, 2002). Previous knowledge suggests that, for a given level of selection relaxation in captivity, the magnitude of the load primarily depends on the residence time of genes in the relaxed environment and the gene flow from captive to wild population (Lynch and O'Hely, 2001), which is in agreement with empirical evidence that success of biological control programs is negatively related to time in captivity (e.g., Myers and Sabath, 1980).

On the other hand, from a demographic view-point, the success of reintroduction should be positively related to the number of released individuals, as demonstrated by theoretical work on demographic stochasticity (e.g., Legendre et al., 1999) and supported by all reintroduction surveys (Griffith et al., 1989; Wolf et al., 1996 ; Fischer and Lindenmayer, 2000). Besides, in naturally fluctuating environments, multi-release reintroductions staggered over several years should improve establishment success (Haccou and Iwasa, 1996).

The demography–genetics trade-off comes from the fact that, in most real reintroduction programs using ex situ techniques, the number of generations spent in benign conditions and the numbers of released individuals are not independent, since a minimal time is necessary to release many individuals. Numerous real reintroduction projects have required several generations of captive breeding in order to reintroduce locally dozens or hundreds of individuals (see, e.g., Schaub et al., 2009, for a case study on the Bearded vulture, and Jule et al., 2008 for numerous examples in carnivores).

Owing to these constraints, short term program duration will imply small numbers of released individuals and subsequently a high risk of short term extinction through demographic stochasticity. In contrast, long program duration may imply the release of

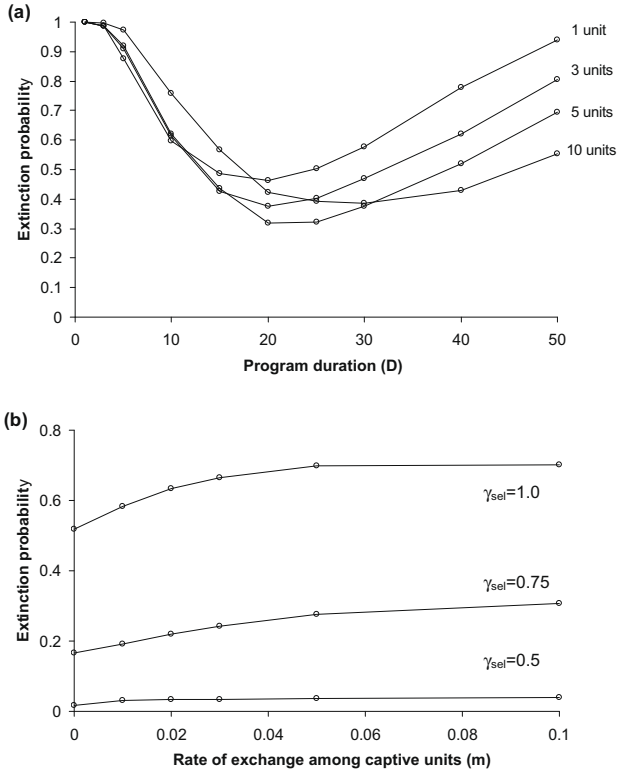

Fig. 4. Influence of the structure of the captive population on projected wild population viability (200 years). Demographic and genetic parameters are presented in Table 1. K_{wild} = 500; R_r = 0.3; γ_{dem} = 2. (a) Population viability as a function of the duration of the reintroduction program (D, in years) and the number of independent captive units. In all cases, the overall number of founders and total carrying capacity of the captive population are, respectively, equal to 35 and 150. m = 0.0; γ_{sel} = 1. (b) Population viability as a function of the exchange rate (m) between captive units for different levels of selection relaxation (γ_{sel}). D = 50 years. Five captive units are considered, with N_{found} = 7 and K_{capt} = 40 in each unit.

more individuals, but involves the risk that genetic deterioration in captivity reduces fitness to a point where the population is no more viable in its natural environment. As a consequence, reintroduction success is maximized for intermediate project duration. The present results demonstrate that such intermediate optimal duration is obtained under a wide range of realistic conditions, although the value of this optimum is highly sensitive to a number of species life history traits and characteristics of the reintroduction protocol.

4.2. Effects of life history traits and reintroduction protocol

A recurrent problem encountered when attempting to integrate demographic and genetic considerations is that demographic and genetic processes do not necessarily act at the same time scale (Robert et al., 2002). Here, short programs (few individuals, high growth rate) result in high short term extinction due to demographic stochasticity, but low longer-term extinction for populations that have survived the first years following reintroduction. The opposite pattern is observed for long programs (see Lande et al., 2003 for general considerations on the distribution of the time to extinction). As a consequence, the optimal program duration greatly varies according to the time horizon considered for assessing reintroduction success (Fig. 1b).

A further complexity comes from the fact that the speed of genetic deterioration in the captive population depends on the species life cycle. Because genetic processes operate on a per-generation basis, gradual genetic processes will be more rapid in a short-lived species than in a long-lived species in terms of absolute time. It follows that, for a fixed duration (number of years), genetic deterioration is less important in long-lived species. The analysis showed indeed that the optimal program duration increases with the species generation length and remains relatively constant across species in terms of number of generations of captive breeding (10–20 generations). Here, most results were obtained using a life cycle with low annual adult survival rates and high annual fecundity rates, typical of passerine (e.g., Garrett et al., 2007) or rodent (Moorhouse et al., 2009) species. For such species, the time scale of the optimal duration is few tens of years (which corresponds to the time scale of conservation planning), but it may correspond to several hundreds of years for long-lived bird or mammal species such as psittaciformes (Brightsmith et al., 2005), falconiformes (Schaub et al., 2009), ungulates (King and Gurnell, 2005) or carnivores (Jule et al., 2008).

As mentioned above, the magnitude of the reduction of fitness in the wild population depends on the residence time of genes in the relaxed environment, but also on the gene flow from the captive to the wild population (Theodorou and Couvet, 2004). Since the balance between the beneficial and negative effects of long program duration will depend on the gene flow, all other management parameters influencing this gene flow (rate of release, sizes of the captive and wild populations) have a quantitative influence on the optimal duration. However, the most important interaction is that between the carrying capacity of the captive population and program duration. If both parameters are large (=strong genetic load + high gene flow), the viability of the reintroduced population may be dramatically reduced.

4.3. Single large or several small?

Many managed or captive populations of endangered species are subdivided in several breeding groups (zoos, arboreta, natural reserves). However, the ecological and genetic effects of subdivisions are multiple and complex, and the current recommendation that several captive populations should be managed as one single random mating population (via regular translocations among institutions) is not based on strong theoretical arguments (see discussion in Frankham, 2008). From a demographic view-point, the division of the captive population into several independent units of the same total size is expected to increase demographic stochasticity and to reduce the long term growth of the captive population, resulting in less released individuals. The genetic consequences of subdivision are more complex. General metapopulation theory indicates that population subdivision is generally detrimental to fitness (Couvet, 2002), although the equilibrium load due to deleterious mutations can be reduced by population subdivision in the case of very recessive alleles (Whitlock, 2002). Unfortunately, existing theory is difficult to apply to the special case of reintroductions and captive breeding, since the average load in captive subunits does not necessarily reflect the resulting fitness of the reintroduced population. The present results indicate that when the captive population is subdivided into completely independent units, selection against mildly deleterious alleles in each unit is indeed less efficient as compared to selection in a panmictic population of the same total size (except in the case of complete selection relaxation, see below), so fitness decreases faster and the fixation of deleterious alleles in each unit is more rapid. However, because genetic drift occurs independently among units, the proportion of mutations fixed at the global scale (i.e., when including individuals from all units) is reduced as compared to one single unit, which facilitates purging of this genetic load in the reintroduced population (see Supplementary Fig. 3). This result is in agreement with the theory predicting that genetic diversity will be higher in a combination of several small populations than in a single large popula-

tion (Lande, 1995) and with expectations on the effect of crosses between inbred lines under the partial dominance theory of inbreeding depression (see Roff, 2002 for discussion and experimental support). Interestingly, several recent experiments on flies have shown that crosses among independent breeding units bred in benign conditions perform much better in non benign conditions than populations from single units (Margan et al., 1998; Woodworth et al., 2002).

So, what is the best strategy? The present results indicate that, if program duration is short (<10–20 generations), the single-unit strategy is generally the best strategy. If program duration is long, the best strategy depends on the level of selection relaxation. In the case of complete relaxation, the average changes in the frequency of deleterious alleles became independent of local population size with the present model (see discussion in Bryant and Reed, 1999), although the variance among simulations increased (results not shown). In this case, a strategy involving several, completely isolated captive units allows improving long term reintroduction success, as compared with several connected units or even one single large unit (in spite of the demographic disadvantage of the several unit strategy). This result remains true as long as the level of selection relaxation is large.

4.4. Study limitation and recommendations

For simplicity sake, a number of important techniques commonly used in the genetic management of captive populations have not been addressed in this study. The equalization of family size (EFS), for example, is one of the most widely used methods to maintain genetic diversity in captive breeding programs. However, EFS has the side effect of reducing the intensity of selection to about one-half (Hill et al., 1996), and its consequences on the reproductive capacity of small populations are still unclear (Rodriguez-Ramilo et al., 2006). Because EFS has multiple and antagonistic consequences, a reliable theoretical assessment of its effects certainly requires modeling jointly, the dynamics of deleterious, neutral and adaptive mutations, which was not achieved here. Similarly, I did not consider the possibility of gene flow from the wild to the captive population. Although this technique is widely used in the context of hatchery populations of salmonids and should, in theory, have beneficial effects on the fitness of supplemented populations (Ford, 2002), it is generally unfeasible for threatened species.

Finally, the assessment of the global effects of these techniques requires the integration of a number of other ecological and evolutionary processes, as well as practical constraints, such as the economic cost of translocations, the risk of disease or parasite spread, Allee effects, or the genetic adaptation to captivity, which is expected to have important effects on reintroduction success for species that have spent several generations in captivity (see Frankham, 2008). In particular, I did not consider the effects of temporal environmentally driven trends in the assessment of the optimal duration of reintroduction programs, although such trends are likely to occur (in both wild and captive populations) at the time scales considered. Presumably, the occurrence of environmental trends may act as an additional source of divergence of the natural and captive environments, which should further reduce the optimal duration of programs.

In spite of these difficulties, two general recommendations emerge from this study.

First, I recommend that captive breeding program durations be minimized to the amount necessary to ensure positive growth of the wild population, and to reach a size compatible with long term persistence. While the durations of most local and regional reintroduction programs are relatively short (typical time scale for conservation planning is 10–20 years), very long-term captive breeding programs are likely to become necessary for an increasing number of species in the future (see Bowkett, 2009), especially for species that are extinct in the wild. If captive breeding program duration exceeds a certain threshold (10–15 generations), it is likely that the genetic cost associated with selection relaxation will overwhelm the demographic benefits of the program, under a wide range of assumptions and parameters. As a second recommendation, if a large number of generations in captivity cannot be avoided, I recommend that captive breeding be conducted in genetically isolated subunits.

Although these two recommendations are deduced on the basis of a simple model that only accounts for one dimension of the problem, they converge with recommendations made on the basis of other models. Minimizing the number of generations in captivity is the best means to minimize inbreeding and genetic adaptation to captivity, and maintaining isolated captive units should permit to minimize disease spread (Ballou, 1993), adaptation to captivity (Frankham, 2008), as well as mortality and economic cost associated with translocations.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.07.016.

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