Demographic Approach to Releasing Adults versus Young in Reintroductions

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Abstract: *Reintroductions are often used for reestablishment of animal populations. The choice of age-class of released individuals, however, is often arbitrary or based on expediency. We developed a demographic model that predicts the relative efficiency of releasing juveniles or adults for a given life cycle. The model accounts for possible reduction of survival and fertility of released adults. It also incorporates demographic and environmental stochasticity to compare release strategies of varying duration and number of releases. We applied the model to the case of reintroduction of Griffon Vultures (Gyps fulvus) in southern France, for which accurate monitoring allowed us to estimate demographic rates and consequences of releases. Overall, for Griffon Vultures, it is more efficient to release adults than juveniles, despite the observed reduction of demographic parameters following release. This approach could be used for the reintroduction of other species.*

Aproximación Demográfica a la Liberación de Adultos Contra Juveniles en Reintroducciones

Resumen: *Las reintroducciones son frecuentemente utilizadas para el restablecimiento de poblaciones animales. Sin embargo, la elección de las clases de edad de los individuos liberados es frecuentemente arbitraria o basada en la conveniencia. Desarrollamos un modelo demográfico que predice la eficiencia relativa de la liberación tanto de juveniles como de adultos para un ciclo de vida determinado. El modelo toma en consideración la posible reducción de la supervivencia y fertilidad de los adultos liberados. También incorpora parámetros aleatorios demográficos y ambientales para comparar las estrategias de liberación según la duración y el número de liberaciones. Aplicamos este modelo en el caso de la reintroducción del buitre leonado (Gyps fulvus) en el sur de Francia, para el cual un monitoreo preciso nos permitió estimar las tasas demográficas y las consecuencias de las liberaciones. En general, para el buitre leonado es más eficiente liberar adultos que juveniles, a pesar de la reducción observada de los parámetros demográficos posteriormente a la liberación. Esta aproximación podría ser utilizada en la reintroducción de otras especies.*

Introduction

Translocations and reintroductions of threatened animals are becoming more numerous, but detailed studies of reintroduced populations are rarely available (Scott & Carpenter 1987; Griffith et al. 1989; Beck et al. 1994; Hodder & Bullock 1997). Due to the lack of information on the consequences of various release strategies, new reintroductions use arbitrary or expedient approaches to select individuals for population restoration. Data collected from well-monitored projects, combined with demographic modeling, can be helpful in making these choices (Saltz & Rubenstein 1995; Bustamante 1996; Green et al. 1996; Bustamante 1998; Saltz 1998). Reintroduced populations thus should be monitored because the data collected allow assessment of the success of these projects and of validity and efficacy of the reintroduction methods (Sarrazin & Barbault 1996, 1997).

Most reintroductions concern flagship or keystone species that are often large and relatively long-lived animals (Wilson & Stanley-Price 1994). One of the main concerns is the choice of the age and number of individ-

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uals to be released. Young individuals, although naturally prone to high mortality, often present the advantage of not being affected by captivity, whereas adults tend to experience higher survival in natural populations but to be affected by captivity. In the same way, many debates on reintroduction strategies focus on the behavior of released individuals or on genetic problems in newly founded populations, but the probability of extinction or the efficiency of a program in terms of demography are rarely discussed.

We considered different release strategies to maximize successful colonization—in the context of population dynamics, the size of the newly settled population. Because the relative effects of demographic stochasticity and genetic events on the viability of small populations have been discussed extensively elsewhere (Lande 1988; Simberloff 1988; Nunney & Campbell 1993; Caughley 1994; Mills & Smouse 1994), we did not consider the genetic context of inbreeding avoidance leading to the choice of individuals. Although some interesting effects on the long-term development of reintroduced populations can be observed (Hartman 1994), we discuss only the way to limit the risk of extinction during the initial phase of population settlement until no further releases are necessary to produce a self-sustaining breeding pool of individuals. Stochastic models showed that extinction probabilities were reduced when adults were released rather than immature individuals for Leadbeater's possum (*Gymnobelideus leadbeateri*; Burgman et al. 1995) or Helmeted Honeyeater (*Lichenostomus melanops cassidix*; McCarthy 1995). Caswell (1989) emphasized that the eventual population was larger at any time if the initial population was concentrated in age-classes with high reproductive values. Nevertheless, because released individuals may suffer short- or long-term reduction in demographic parameters (called "release costs" in the sequel), the use of reproductive values estimated from nontranslocated individuals may not predict the size of translocated populations.

We investigated the consequences of two alternatives—release of young versus release of adults—in a general framework and illustrated our models with the case of the successful reintroduction of a population of Griffon Vultures (*Gyps fulvus*) in southern France. We compared the efficiency of these strategies in terms of population sizes at each time step to determine which release costs were acceptable and chose the reintroduction strategy that led to the largest population size. We used this general model to investigate the effects of interactions between life-history traits and release costs on the eventual population size of reintroduced species. Using the case of the Griffon Vulture, we incorporated demographic and environmental stochasticity in the models and assessed the consequences of the number of released individuals per year and the duration of releases on extinction probabilities. Finally, we discuss the effect of adult or juvenile releases on the age structure of the reintroduced population.

Methods

Population Modeling

As a first step, we modeled the life-cycle of the natural population based on its life-history traits. The parameters were α, age at first breeding; s_0, annual juvenile survival; s_1, s_2, ..., $s_{\alpha-1}$, survival rates during immaturity; v, adult survival rate; and f, fertility. Fertility included the proportion of breeders γ, the productivity P defined as the number of fledged young per breeding pair per year, and the juvenile survival rate s_0. Juvenile and immature survival rates were lower than the adult survival rate. We as-
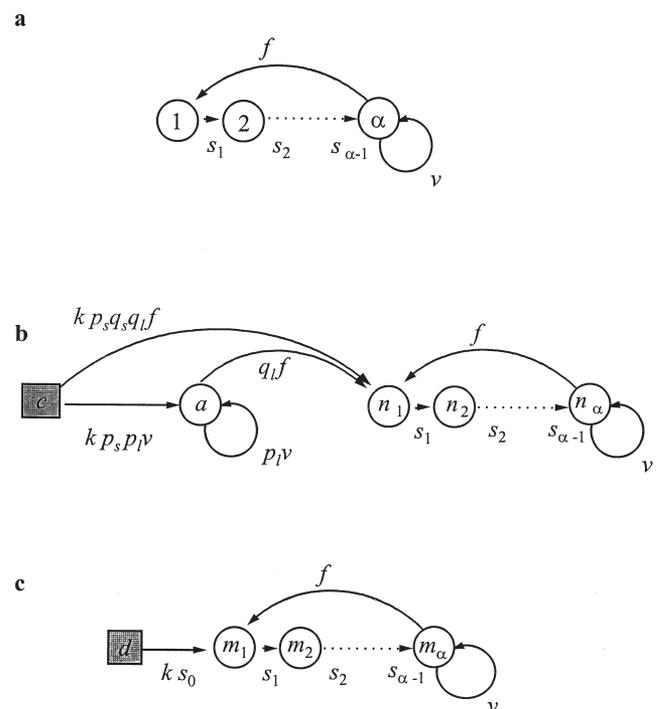
Figure 1. Age-structured, life-cycle graph and release strategies used in the general model: (a) natural life-cycle graph (1, age 1 year; 2, age 2 years; ...; α, adults; f, fertility [f = 0.5 × proportion of breeders × productivity × juvenile survival]; s_1, s_2, ..., $s_{\alpha-1}$ immature survival rates; v, adult survival rate); (b) release of adults (c, captive adults; k, number of yearly released individuals; a, released adults; costs of release on demographic parameters expressed through p_s, p_l, short- and long-term survival ratios, and, q_s, q_l, short- and long-term fertility ratios, respectively; n_1, n_2, ..., n_α, wild-born individuals aged 1 year, 2 years, ... or adult); (c) release of juveniles (d, captive juveniles; s_0, juvenile survival rate; m_1, m_2, ..., m_α, individuals aged 1 year, 2 years, or adults, no costs of release).

summed the growth rate λ of the natural population to be >1 (otherwise no reintroduction would be attempted). Demographic parameters were not sex-dependent. The life-cycle graph corresponded to a prebreeding census (Fig. 1a; Caswell 1989; MacDonald & Caswell 1993).

Reintroduction Strategies

Because demographic parameters define the life cycle of the species, we considered release parameters (k, t_r, p, q) to define reintroduction strategies. The vulnerability of any population is directly linked to its size (Caughley 1994). In that context, we modeled and compared the dynamics of two reintroduced populations of size $n(t)$ and $m(t)$ at time t, differing respectively by the yearly release of k adults (strategy A) or k juveniles (strategy J) up to time t_r. Strategy A (Fig. 1b) resulted from the release of adults in year $t = 0$ just before breeding in the wild. Possible costs of release were expressed by means of release ratios p on survival and q on fecundity; in other words, adult survival rate was reduced by a factor p after release, and fertility was reduced by a factor q after release. The maximum costs were achieved for ratios equal to 0; the minimum costs corresponded to ratios equal to 1. For both survival and fertility, we considered short-term costs immediately after release using ratios p_s and q_s respectively, and long-term costs during the lifespan of released individuals using ratios p_l and q_l, respectively. The same kind of analyses could be run for other time courses. For clarity we focused only on the effects of short- and long-term costs on the efficiency of different release strategies. We assumed that release costs were not transmitted from released adults to their offspring. For strategy A, the matrix model corresponding to the life-cycle graph (Fig. 1b) was

$$
\begin{pmatrix} c \\ a \\ n_1 \\ n_2 \\ \vdots \\ n_\alpha \end{pmatrix}_{t+1} = \begin{pmatrix} 1 & 0 & 0 & & \cdots & 0 \\ k(t)p_sp_lv & p_lv & 0 & & \cdots & 0 \\ k(t)p_sq_sq_lf & q_lf & 0 & 0 & \cdots & f \\ 0 & 0 & s_1 & 0 & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & & \vdots \\ 0 & 0 & 0 & \cdots & s_{\alpha-1} & v \end{pmatrix} \begin{pmatrix} c \\ a \\ n_1 \\ n_2 \\ \vdots \\ n_\alpha \end{pmatrix}_t . \quad (1)
$$

The upper diagonal block corresponded to introduced adults with $k(t) = k$ for $t = 0, \cdots, t_r - 1$ and $k(t) = 0$ for $t \geq t_r$. The lower diagonal block corresponded to wild-born individuals. In the population vector, c corresponded to the captive stock, a was the number of introduced adults, and n_i the number of wild-born individuals in the ith age class. Initial values were 1 for the captive stock c and 0 for other classes. Population size at time t was $n(t) = a(t) + n_1(t) + \cdots + n_\alpha(t)$.

Strategy J resulted from maintaining adults in captivity and releasing their offspring just after breeding in year $t =$

0. For strategy J, we assumed no cost of captivity on demographic parameters (Fig. 1c). The matrix model was

$$
\begin{pmatrix} d \\ m_1 \\ m_2 \\ \vdots \\ m_\alpha \end{pmatrix}_{t+1} = \begin{pmatrix} 1 & 0 & 0 & \cdots & 0 \\ k(t)s_0 & 0 & 0 & \cdots & f \\ 0 & s_1 & 0 & \cdots & 0 \\ \vdots & \vdots & \ddots & & \vdots \\ 0 & 0 & & s_{\alpha-1} & v \end{pmatrix} \begin{pmatrix} d \\ m_1 \\ m_2 \\ \vdots \\ m_\alpha \end{pmatrix}_t . \quad (2)
$$

In the population vector, d corresponded to the captive stock, and m_i was the number of wild-born individuals in the ith age class. Initial values were 1 for the captive stock d and 0 for other classes. Population size at time t was $m(t) = m_1(t) + \cdots + m_\alpha(t)$.

Simulations

Simulations were performed with the ULM computer program designed by Legendre and Clobert (1995). This software allows study of general population dynamics models, both deterministic or stochastic (Legendre & Clobert 1995; Ferrière et al. 1996). Deterministic matrix models were used to study the efficiency of strategies A and J in terms of population sizes with time for different patterns of release ratios and different life cycles. Stochastic two-sex models were used to investigate extinction probabilities. Demographic stochasticity comes from the probabilistic run of the life cycle by individuals and assigns population sizes to integer values. For example, if N individuals were subjected to a survival rate s, then the number of survivors was computed as the trial of the binomial distribution $B(N,s)$. We used a two-sex model, with the same demographic parameters for males and females and a balanced sex ratio. We computed the number of breeders nb using the binomial distribution, $B(u,\gamma)$, with u the minimum number of males and females and γ the proportion of breeders.

In the example of the Griffon Vulture, clutch size was initially one egg, and demographic stochasticity resulted in either 0 or 1 egg; therefore, the number of fledglings produced by a number nb of breeders having a productivity P was computed with the binomial distribution $B(nb,P)$. In the same way, the sex of the fledglings was randomized according to a 0.5 primary sex ratio. For environmental stochasticity, each demographic parameter x was obtained from a normal distribution with a mean value estimated in the field x_f and standard deviation σ_x. Both strategies were subjected to the same random variation of demographic parameters. Because the reintroduction of Griffon Vultures in southern France occurred in a favorable environment, we considered that estimates of demographic parameters x_f were at their maximum, so only negative events were simulated. Thus, demographic distributions were truncated (i.e., when the value of x was higher than x_f, it took x_f). In our data no significant variation of demographic parameters was ob-

served with time (Sarrazin et al. 1994, 1996). Consequently, σ_x values were chosen with the consideration that a well-restored environment should entail a low variance in parameters with high growth-rate sensitivity and a higher variance in parameters with low growth-rate sensitivity.

Growth-rate sensitivity and elasticity to demographic parameters may be estimated from matrix models (Caswell 1989; Ferrière et al. 1996). Because we used a normal distribution and truncated the values, σ_x was not the actual standard deviation of the values used in the model. The statistical behavior of the population for each reintroduction strategy was obtained via Monte Carlo simulations: 1000 population trajectories were drawn over 50 years. Extinction probabilities were computed as the number of extinct trajectories over the total number of trajectories. A population was considered extinct when it contained no individual. Because of limiting factors such as food resources or breeding sites, no reintroduced population can grow exponentially without experiencing density dependence. Nevertheless, because extinction probabilities decrease quickly with an increase in population size, the first years following release are the main concern, and we did not consider density dependence.

The Griffon Vulture Reintroduction

The reintroduction of Griffon Vultures in southern France provided useful empirical data for our model because of accurate monitoring of the newly restored population. Details on the historical extinction and restoration of this population have been related by Bonnet et al. (1990), Terrasse et al. (1994), Sarrazin et al. (1994, 1996), and Sarrazin (1998). From 1980 to 1986, 61 individuals (59 marked) were released in the Causse Méjean. Contrary to the practice in other raptor reintroduction programs, only adult birds were released from 1981 to 1983 (age ≥4 years, 39 individuals). From 1983 onward, 20 immature and subadult birds (0–3 years old) were released. Introduced birds started breeding in the wild in 1982, and since then released birds have established a breeding colony from which more than 275 young had been produced by 1998. The colony currently contains more than 250 birds. These vultures feed mainly on sheep carcasses from local farms, which are provided at artificial feeding sites, although feeding on natural carcasses has become more frequent during recent years. The accurate monitoring of the population allowed us to estimate survival using capture-mark-resighting methods, reproduction parameters, and release ratios for the first 10 years following the releases (Table 1; Sarrazin et al. 1994, 1996). Demographic parameters estimated for birds born in the wild were used to simulate those of released juveniles because only four birds were released in

Table 1. Demographic parameters for a reintroduced population of a long-lived species (Griffon Vulture) and for a naturally increasing population of a short-lived species (Dipper).

Parameter	Griffon Vulture[a]	Dipper[b]
Juvenile survival (s_0)	0.858	0.2
Immature survival (s_1, s_2)	0.858	—
Subadult survival (s_3)	0.987	—
Adult survival (v)	0.987	0.6
Age at maturity (α)	4	1
Proportion of breeders (γ)	0.8	1
Productivity (P)	0.818	4.4
Short-term survival ratio (p_s)	0.752	—
Long-term fertility ratio (q_l)	0.509	—

[a]Data from Sarrazin et al. (1994, 1996).
[b]Data from J. Clobert (personal communication).

their first year. Moreover, initial competition with adults may have been low due to the high availability of food resources and nest sites during this period.

Results

Comparison of Release Strategies

The demographic consequences of releasing adults (strategy A) or juveniles (strategy J) were assessed by computing, at each time step t, the population sizes $n(t)$, $m(t)$ for any combination of the release ratios p, q with short- or long-term durations. A family of isoclines (I_t) for $n(t) = m(t)$ could be computed from the life-cycle parameters of the species and for any release duration (Appendix). These isoclines were used to determine which reintroduction strategy was more efficient according to possible demographic costs of releases expressed through the release ratios p, q (Fig. 2). When strategy A had given release ratios p, q, we considered the position of point (p, q). If point (p, q) was on the right side of isocline I_t, we had $n(t) > m(t)$, and strategy A was better than strategy J at time t. If point (p, q) was on the left side of I_t, J was better than A at time t. For large t, we had an asymptotic isocline I_∞. When there was no cost for strategy A, we had $n(t) > m(t)$ for all t because adults survived better ($s_0 \leq v$) and reproduced sooner: point (1,1) was on the right side of I_∞. More generally, there was always a set of points (p, q) on the right of all isoclines I_t. When strategy A had such release ratios, it was better than strategy J at any time. We explored four cases using the Griffon Vulture's life cycle.

Short-term ratio on survival (p_s) and long-term ratio on fertility (q_l): The isoclines I_t obtained in this case (Fig. 3a) showed a complex variation with time for the effects of the release ratio p_s, q_l on the relative efficiency of both release strategies. The efficiency of strategy A compared to strategy J increased during the release period—5 years in this example—and slowly decreased thereafter. This model corresponded to the situation observed in the
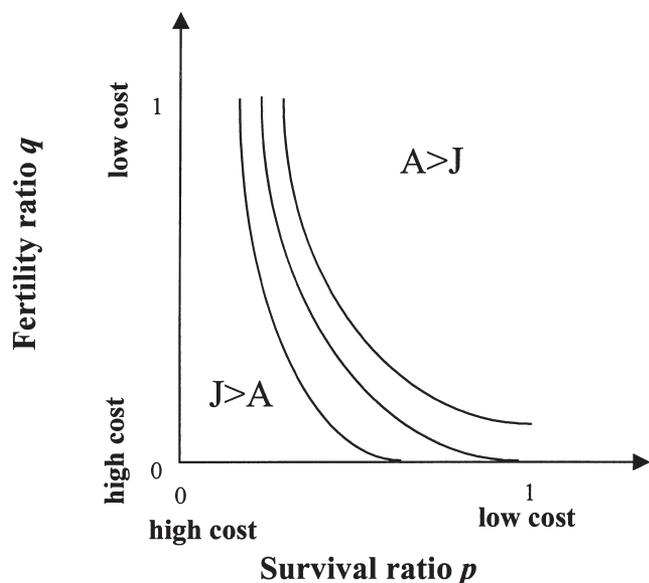
Figure 2. Isoclines for assessing the relative efficiency of adult release or juvenile release strategies. Release costs are considered for release of adults (strategy A) but not for release of juveniles (strategy J): p, *survival ratio = reduced survival /natural survival;* q, *fertility ratio = reduced fertility /natural fertility; a point (*p, q*) located on the right of an isocline* I_t *corresponds to a larger population size at time* t *for strategy A (*n(t) > m(t)*); a point (*p, q*) located on the left of an isocline* I_t *corresponds to a larger population size at time* t *for strategy J (*n(t) < m(t)*).*

Griffon Vulture reintroduction in Southern France with the estimated values of release ratios being respectively $p_s = 0.752$ and $q_l = 0.509$ (Table 1). In this case, the effect on fertility was detected with a reduction of productivity (Sarrazin et al. 1996). According to Fig. 3a, except for the first year of releases, strategy A was always better than strategy J, showing the relevance of the actual management of this program.

Long-term (p_l *and* q_l*) and short-term (*p_s *and* q_s*) release ratios*: When the effects on survival and fertility were permanent, the efficiency of strategy A was reduced compared to that of strategy J (Fig. 3b). In case of small effects of captivity (high values of p_l and q_l), however, strategy A remained more efficient than strategy J.

When the effects on survival and fertility were considered on a short-term basis, the disadvantage of releasing adults decreased quickly up to 1 year after the last releases, and the difference between the two population sizes remained constant thereafter (Fig. 3c). Isoclines I_t were almost vertical, showing the sensitivity of the result to effects on survival compared to those on fertility.

Long-term survival ratio (p_l*) and short-term fertility ratio (*q_s*)*: Isoclines I_t obtained in this case (Fig. 3d) showed that strategy J was more efficient than strategy A. When p_l

was higher than 0.87 and for all q_s, strategy A was better than strategy J. As in the previous case (Fig. 3c), for any value of q_s there exist values of p_s which ensure a better efficiency for strategy A. In the same way, isoclines I_t were almost vertical, showing the sensitivity of the result to effects on survival compared to those on fertility.

Release Strategies and Life Histories

To apply our model to species presenting different life-history traits, we simulated the effect of the release ratios p and q on the relative efficiency of adult and juvenile release strategies for a long-lived species (Griffon Vulture; Fig. 3a) and for a short-lived one (Dipper [*Cinclus cinclus*]; Table 1; Fig. 4) for a release duration of 5 years. For both species, we considered the effects of a short-term release ratio on survival and those of a long-term release ratio on fertility, as observed in the field for Griffon Vultures. It appeared that the release of adults was efficient, with lower release ratio p_s and q_l for the short-lived than for the long-lived species, for which the area of adult release efficiency remained relatively wide. The pattern of isoclines for both species showed that population growth for both strategies would have been difficult to compare empirically.

Extinction Probabilities and Age Structure

Using the Griffon Vulture example, we estimated extinction probabilities for both release strategies with demographic stochasticity. Overall, extinction probabilities quickly decreased with the number of yearly releases k as well as with the duration of the releases t_r (Fig. 5a). Despite effects on the survival and fertility of released adults, extinction probabilities were higher for releases of juveniles. When environmental stochasticity was taken into account (Table 2), extinction probabilities increased, but strategy A remained less risky than strategy J (Fig. 5b). Finally, we considered the consequences of a stochastic variation from the initial sex ratio in the case of strategy J (Fig. 5c). Indeed, in strategy A, pairs may be constituted in captivity, and the number of individuals of each sex released per year may be controlled. On the contrary, the sex of released juveniles may be difficult to assess, and even their availability cannot be corrected by keeping individuals in captivity from one year to the next. Including stochastic variation of the actual sex ratio of released juveniles notably increased the extinction probabilities for strategy J (Fig. 5c).

For species in which sociality may play a role in foraging and breeding, the effect of release strategy on age structure may be important. In the case of the Griffon Vulture, the simulation of releases of six individuals per year over 5 years showed that releases of adults (Fig. 6a) and releases of juveniles (Fig. 6b) give different results. Strategy A led to a stable age distribution later than strat-
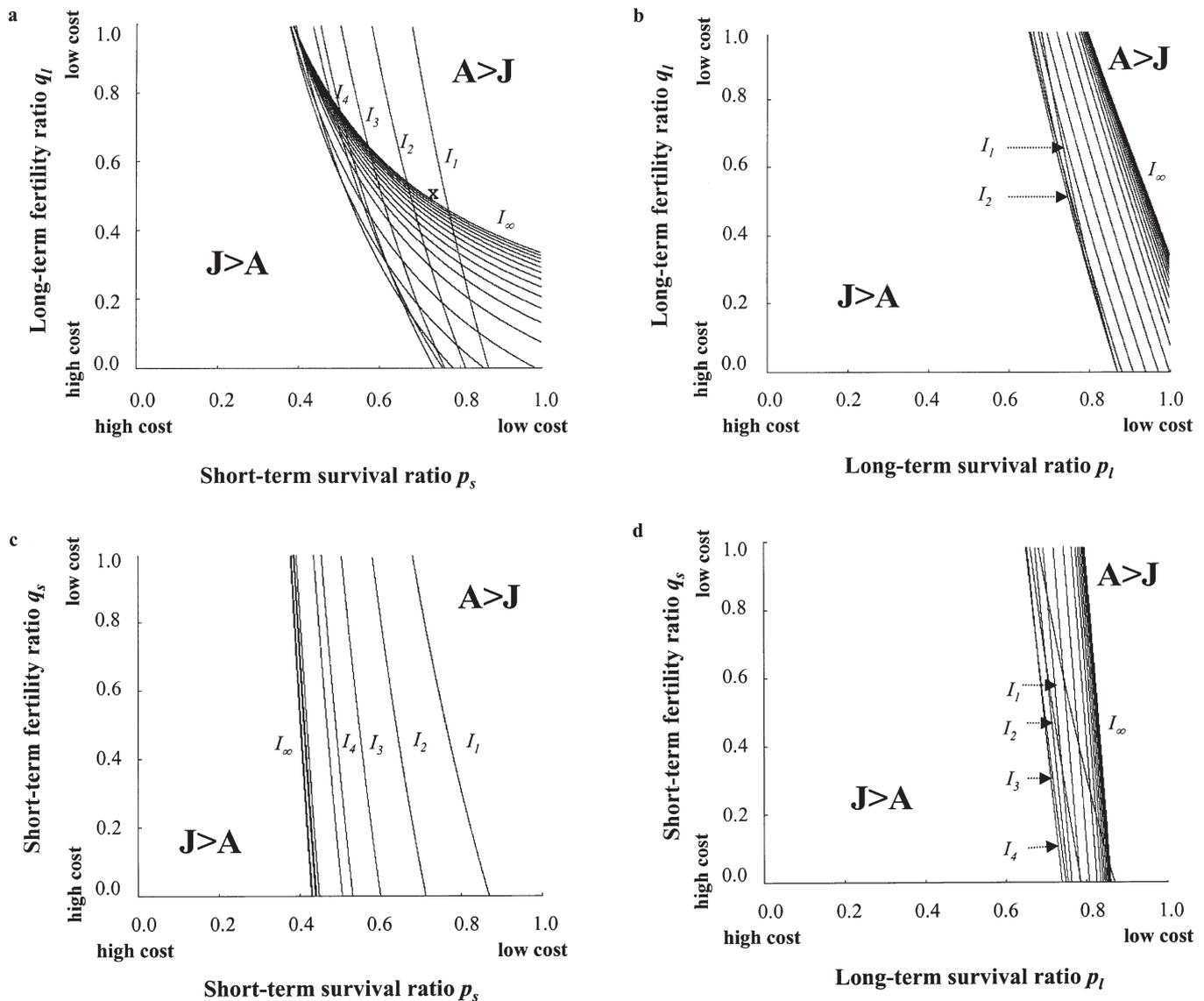
Figure 3. The general model described in Fig. 2 applied to the life cycle of the Griffon Vulture (Gyps fulvus) for a release period of 5 years: (a) short-term survival ratio p_s and long-term fertility ratio q_l (the X shows the observed values of p_s and q_l); (b) long-term release ratios p_l and q_l; (c) short-term release ratios p_s and q_s; and (d) long-term survival ratio p_l and short-term fertility ratio q_s.

egy J, but with reduced transient effects. Indeed, releasing juveniles entailed more important changes in age structure and thus in social environment at an early stage.

Discussion

Our results show that the release of adults may be the most efficient strategy in case of low expected release costs for long-lived species. Similarly, our results suggested that higher values for release costs can be sustained for short-lived species. The value and the causes of these costs may vary greatly, however, according to the species and the management of the reintroduction program. Such costs should therefore be documented carefully.

Reduced Survival and Reproduction after Release

In the Griffon Vulture reintroduction, survival of released adults was reduced immediately after release, but previously captive adults survived as well as wild-born adults thereafter (Sarrazin et al. 1994). By contrast, permanently reduced breeding capacities did not prevent birds from staying in the released population and thus could still be observed years after the end of releases (Sarrazin et al. 1996). Release costs did not appear to af-
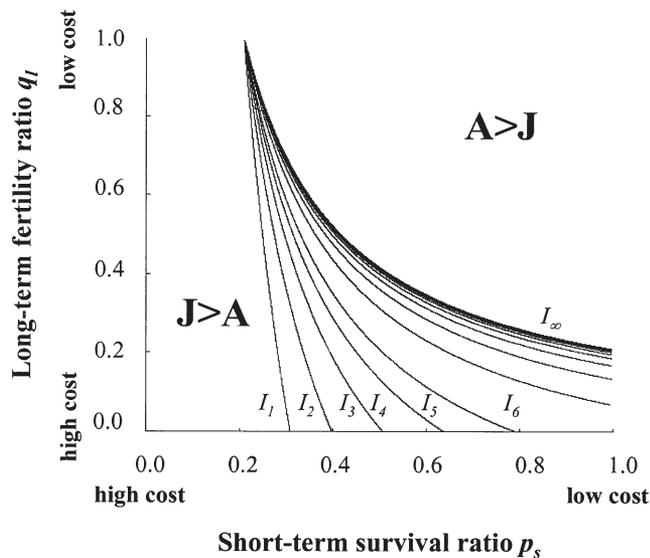
Figure 4. The general model described in Fig. 2 applied to the life cycle of a short-lived species (Dipper, Cinclus cinclus) *for a release period of 5 years, with short-term survival ratio* p_s *and long-term fertility ratio* q_l.

fect the following generation, which exhibited good breeding success and survival.

The lack of comparison with demographic parameter estimates in other reintroduction projects prevents us from generalizing from the duration and value of these costs. Nevertheless, it seems that high mortality during the initial period after release is characteristic of many reintroductions (Fyfe 1978; Kleiman 1989; Ralls et al. 1991; Beck et al. 1994; Shepherdson 1994). Several examples may be found for a wide range of taxa. Carnivores such as European lynx (*Lynx lynx*), red wolf (*Canis rufus*), or otters (*Lutra lutra*) reintroduced from captive breeding or translocated from wild populations generally suffered high mortality after release, even in successful restorations (Moore & Smith 1991). The mortality of swift foxes (*Vulpes velox*) reintroduced in Canada occurred mostly within the first month after release and was stronger for captive-raised than for wild-caught individuals (Carbyn et al. 1994). In the golden lion tamarin (*Leontopithecus rosalia*) reintroduction in Brazil, individuals were lost immediately after releases (Kleiman et al. 1991), but young zoo-born individuals survived better than older ones, and wild-born young adapted more quickly than their zoo-born parents. Tule elks (*Cervus elaphus nannodes*) suffered similar reductions in calving rates and adult survival after introduction (Gogan & Barrett 1987). Similarly, Asiatic wild ass (*Equus hemionus*) showed low survival but also low reproductive success following reintroduction, which were linked to the stress caused by capture, transport, and release procedures (Saltz & Rubenstein 1995).
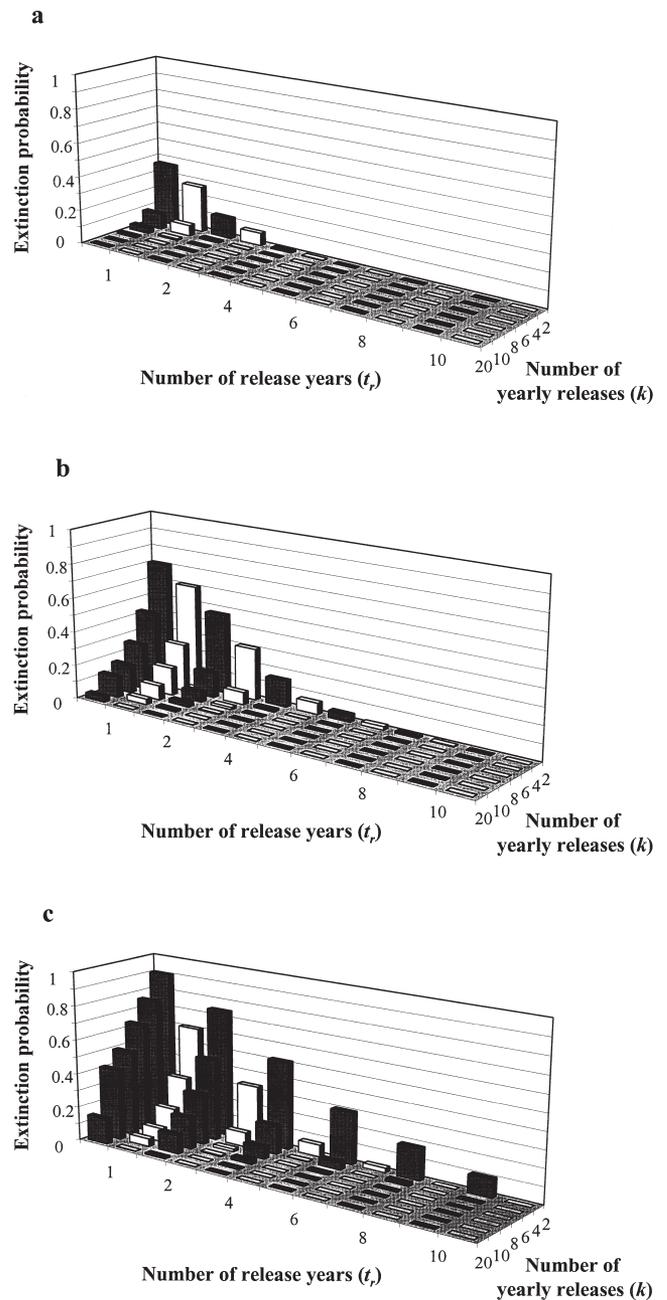
Figure 5. Extinction probabilities for releases of juveniles (black bars) or adults (white bars) of Griffon Vulture according to the duration of releases (t_r*) and the number of yearly releases (*k*): (a) demographic stochasticity only; (b) demographic and environmental stochasticity; and (c) same as (b) but including stochastic variation in juvenile sex ratio at time of release.*

Moreover, basic experiments on nonthreatened species provide similar results. Massot et al. (1994) introduced common lizards (*Lacerta vivipara*) into already occupied habitat (not strictly a reintroduction) and showed that translocated individuals had a higher mor-

Table 2.   Demographic parameters of Griffon Vultures with environmental stochasticity.

Parameters	Mean value	SD
Juvenile survival (s_0)	0.858	0.3
Immature survival (s_1)	0.858	0.2
Immature survival (s_2)	0.858	0.1
Subadult survival (s_3)	0.987	0.05
Adult survival (v)	0.987	0.05
Productivity (P)	0.818	0.3

tality rate immediately after the introduction, except for juveniles. In the same way, carabid beetles (*Abax ater* and *Petrostichus madidus*) translocated for competition assessment suffered strong mortality rates likely associated with a lack of adaptation to local conditions (Loreau 1990).

Natural Demographic Consequences of Translocation

Reductions in survival and fertility following release result from the interaction of the genotype and phenotype of released individuals with their new environment. Even without considering any alteration of these three factors, as in translocation of wild-born individuals, reintroduction may entail problems of local adaptation because released individuals generally originate from various populations differing from the extinct one. Translocations into the core of a species' historical range appear to be more successful than those to the periphery or outside of historical ranges (Griffith et al. 1989; Wolf et al. 1996). This might reflect the importance of leading reintroductions into habitats providing selection pressures (for example, pathogens or parasites; Woodford & Kock 1991; Viggers et al. 1993) to which released individuals are adapted. Moreover, as Massot et al. (1994) underlined, translocation does not simulate the three parts of natural dispersal—departure, transient phase, and settlement phase—but only the last one. It is likely that, when the ability to disperse varies among members of a population, the ability to face and colonize a new habitat also varies among individuals. In this context, part of the observed effects, particularly on survival, might reflect some selection for colonizing ability.

The values of effects on survival and fertility are likely to be closely linked to the importance of behavioral and social aspects of feeding and breeding in the reintroduced species, and they are influenced by the age structure of the released group (Lyles & May 1987; Stanley Price 1989*a*, 1989*b*; May 1991; Shepherdson 1994; Komdeur & Deerenberg 1997). Stanley Price (1989*b*) underlines the role of social organization and the interest of releasing entire social groups with a combination of different age classes to increase reintroduction success. One hypothesis underlying the release of juveniles is the philopatry of released young. It might be impor-

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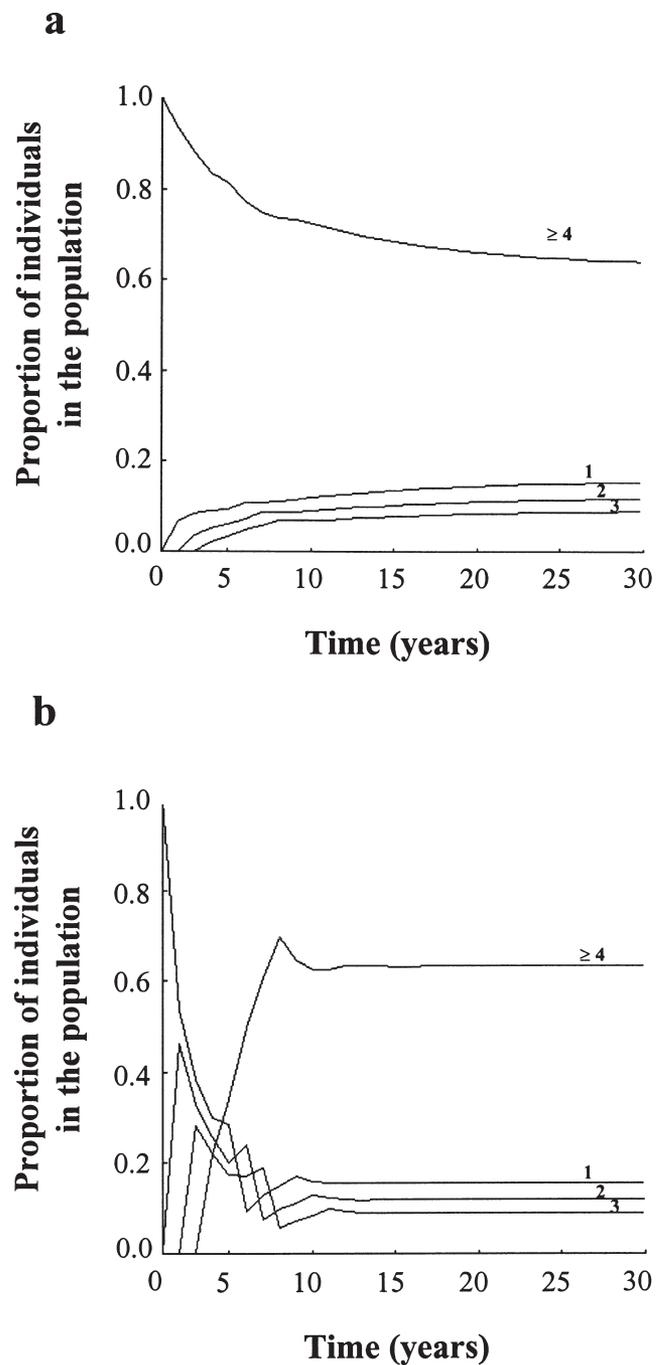
Figure 6. Population age structure (ages above lines) over time in the release of 6 Griffon Vultures per year over 5 years: (a) release of adults and (b) release of juveniles.

tant to consider the spatial scale at which philopatry is likely to occur in order to restore and conserve the release area at this scale. For example, the average distance between releases and return sites of young Peregrine Falcons (*Falco peregrinus anatum*) released in southern Canada was 130 km; females tended to travel farther than males (Holroyd & Banasch 1990). Moreover,

first-reintroduced individuals face, by definition, an environment without conspecifics. Therefore, any mechanism involving conspecific attraction in apparent philopatry cannot be achieved, and only individual imprinting toward the release site may play this role. In this way, coloniality is an argument for adult releases. The study of colony settlement in the Griffon Vulture reintroduction suggested that conspecific attraction (Stamps 1988; Smith & Peacock 1990) played a role in the recruitment of young individuals (Sarrazin et al. 1996). This process has already been emphasized as a useful tool to fix translocated individuals for conservation (Reed & Dobson 1993). In the same way, released adults may be encouraged to settle by mimicking the presence of conspecifics; for example, Puffins (*Fratercula arctica*) released as young were encouraged to settle by putting dummy individuals in the release area (Kress & Nettleship 1988), and Griffon Vultures were encouraged with artificial nests (Terrasse et al. 1994). Finally, releases at the beginning of the breeding season can increase the probability that the released adults will actually settle in the area.

Human Effects on Release Strategies

Besides the natural stress caused by translocation, stress may also result from artificial modification of the genetics and behavior of released animals as well as of target habitat. First, despite the fact that reintroduction should occur only in a restored habitat, causes of extinction are often difficult to define and eradicate (Griffith et al. 1989; MacKinnon & MacKinnon 1991; Wolf et al. 1996). Second, the reduced fitness of released individuals may be reinforced by influences of the captive-breeding history of their ancestors on their genetic traits. The absence of natural selection pressures or the presence of artificial constraints on breeding in the captive environment, combined with a low number of founders, are often identified as important risks of inbreeding and genetic drift, which are likely to entail the failure of reintroduction projects (Ballou 1991; Lacy 1994; Ebenhard 1995). For example, the negative effect of inbreeding on the survival of white-footed mice (*Peromyscus leucopus*) after their experimental reintroduction was strong (Jimenez et al. 1994). Nevertheless, it may be difficult to predict the consequences of genetics on the survival or reproduction of individuals released as young or adults. Therefore, because our general model ignored such possible costs for released juveniles, it might be considered optimistic for the release of young and pessimistic for the release of adults. Despite this, we showed that releasing adults remains the most efficient strategy in a range of cases.

Third, the phenotype of individuals may have been altered by numerous causes before release. High immunological screening during captivity may reduce the ability

of released individuals to face pathogens in their new environment (May 1991; Viggers et al. 1993). Such pathogens could therefore have more effect on released adults than released young (Lyles & May 1987). Moreover, one of the main arguments for releasing juveniles instead of adults is that the ontogeny of behavior may be affected by captivity (Curio 1996; McLean 1997). This alteration of behavior might be due to imprinting on humans. For example, MacKinnon and MacKinnon (1991), working on orangutans (*Pongo pygmaeus*), showed that captive individuals, even young, may have no fear of people and may become pests after release. Impaired behavior, however, may also be the consequence of an absence of natural stimuli during development. Captive-bred individuals released as adults may suffer limitations in their learning abilities and therefore show reduced survival (May 1991; Shepherdson 1994). For example, primates facing new habitats have to learn to orient and move themselves in space, to forage, to obtain suitable places to rest and sleep, to interact with other species (e.g., predation avoidance), and to interact with conspecifics for competition, cooperation, mate choice, or rearing of offspring (Kleiman 1989; Box 1991). It is likely that captivity may affect the success of reintroduction of any species in which such behavioral traits depend on learning. Moreover, the success of reintroduction of many migratory birds and mammals may rely on their learning ability in finding new migration routes (Ounstead 1991).

Concerning foraging, the diet provided during captivity to Mississippi Sandhill Cranes (*Grus canadensis pulla*) induced foraging differences between native and released birds in a context of population reinforcement (Zwank et al. 1988). The fact that, in our example, Griffon Vultures are scavengers feeding in groups allowed the reintroduction team to use supplementary feeding, which probably increased the birds' survival (Sarrazin et al. 1994). Real predators such as raptors could face problems in developing foraging and feeding abilities after a long period in captivity. This is why releasing juveniles by the hacking method (Temple 1978) is generally recommended for reintroducing raptors. Most alteration of behavior due to captivity should not be found in released young. Biggins et al. (1998), however, showed experimentally that, after-release, the survival of young black-footed ferrets (*Mustela nigripes*) was strongly influenced by the quality of their rearing environment. Moreover, parent-offspring relationships during captivity may also be modified by captive-rearing methods. To increase the reproductive rate of captive individuals, artificial breeding and rearing of young often involve puppets or surrogates and fostering or cross-fostering, but the consequences of these techniques on the breeding ability of released young could vary according to species (Cade & Temple 1995). Moreover, the cultural transmission of behavioral traits may be disrupted if young indi-

viduals are isolated from parents before acquiring such traits (McLean 1997).

To reduce these release effects on behavioral alteration, pre- and post-release training have been employed, and the enrichment of the captive environment to mimic the natural one has been proposed (Kleiman 1980; Box 1991; Shepherdson 1994; McLean 1997). Ellis et al. (1978) trained Masked Bobwhite (*Colinus virginianus ridgwayi*) before release to improve survival and avoid predation by dogs and humans. Temple (1978) compared the release of adult birds of prey to the release of juveniles by the hacking method and found that the survivorship of birds held in captivity was reduced when prerelease training was not provided. Despite determining that hacking might be successful, however, he pointed out the lack of protection against predators by parents of birds released by hacking and also the premature dispersal of released juveniles.

Management of Release Strategies

Considering a priori the possible consequences of release strategies for the dynamics of reintroduced populations is an important element of reintroduction preparation (Sarrazin & Barbault 1996). Nevertheless, the management of reintroduction programs encounters many constraints that often interact with purely biological arguments. For example, the availability of individuals to be released may vary greatly among species. It has been argued that reintroduction should not jeopardize the captive population in order to avoid total extinction in the wild (Kleiman et al. 1994). In the case of adult release, the delay necessary to get a sufficient number of mature individuals (e.g., from available young) may be a constraint, but it can be used efficiently. A strictly balanced sex ratio may be controlled, and pairs may be constituted in captivity with respect to mating strategies (Kleiman 1980). If this cannot be achieved when juveniles are released, extinction probabilities resulting from this strategy clearly increase (Fig. 5c). Furthermore, captivity until age at maturity can constitute a useful period in which to acclimatize individuals to the release area, to achieve a soft release, and to reduce the stress causing short-term release costs (Kleiman 1989; Bright & Morris 1994). In the same way, this period can be used to complete the preparatory phase of habitat restoration, a crucial period for reintroduction success (Stanley-Price 1989*a*, 1989*b*; Kleiman et al. 1994), and to educate local human populations in order to increase conservation efficiency (Reading & Kellert 1993).

Finally, another advantage of releasing adults is that the suitability of the habitat or the ability of released individuals to breed can be checked immediately after the release, which would not be the case for young because of delayed maturity. In fact, one of the short-term criteria of reintroduction success might be the production of a wild-born generation as soon as possible. Kleiman et al. (1991) suggested that released zoo-born adults might be "living in a wild zoo and that their purpose is to produce and provide offspring that will be truly self-sustaining." In that context, our model may help simulate various scenarios of release. The use and improvement of this kind of model depends on the accurate assesment of reintroduced population dynamics. Therefore, this a priori approach of reintroduction design encourages more monitoring of reintroduced populations, particularly from a demographic point of view.

Acknowledgments

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Appendix

Practical Method for Comparing Release of Adults versus Juveniles

We compared the release of adults (strategy A) and the release of juveniles (strategy J) in terms of the respective population sizes at time t, $n(t)$, and $m(t)$.

Running in parallel matrix model 1 for strategy A and matrix model 2 for strategy J allowed us to compare population sizes $n(t)$ and $m(t)$ at each time step for any value of the release ratios p_s, p_l, q_s, q_l. It was convenient to compare the strategies with only two of the release ratios considered as parameters. For example $p = p_s$ and $q = q_l$ were allowed to vary between 0 and 1, whereas p_l and q_s were fixed. We computed analytical expressions 3 and 4 below, from which release isoclines I_t could be built. A point (p, q) on I_t was such that, at time t, release ratios p, q, lead to $n(t) = m(t)$. A point located on the right of I_t was such that strategy A was better that strategy J at time t ($n(t) > m(t)$). A point located on the left of I_t was such that strategy J was better than strategy A at time t ($m(t) > n(t)$).

ISOCLINES WITH q_l AS A FUNCTION OF p_s OR p_l

Models 1 and 2 allowed us to compute n (depending on p_s, p_l, q_s, q_l), the number a of introduced adults, and m. For strategy A, individuals born in the wild were in number $n - a$. Because they were descendants of the introduced adults reproducing with long-term fertility ratio q_l, we had $n - a = q_l b$, where b did not depend on q_l. Looking for the equilibrium value $\tilde{q}_l$ leading to a population size $\tilde{n}$ such that $\tilde{n} = m$, we solved

$$\tilde{n} = a + \tilde{q}_l b = a + \tilde{q}_l \frac{n-a}{q_l} = m,$$

giving

$$\tilde{q}_l = q_l \frac{m-a}{n-a}. \qquad (3)$$

In fact, $\tilde{q}_l$ depended only on p_s, p_l and q_s because q_l canceled in equation 3. For any value p_l of the long-term survival ratio, or any value p_s of the short-term survival ratio, the corresponding value $\tilde{q}_l$ of the fertility ratio on the isocline could be computed using equation 3.

ISOCLINES WITH q_s AS A FUNCTION OF p_s OR p_l

For strategy A, k introduced adults produced $k p_s q_s q_l f$ offspring the first year of release. This offspring and their descendants numbered as if $k p_s q_s q_l f$ individuals instead of $k s_0$ individuals were introduced according to strategy J. Their number was therefore

$$p_s q_s q_l f \frac{m}{s_0},$$

and we had

$$n = a + p_s q_s q_l f \frac{m}{s_0} + b,$$

with a the number of introduced adults and

$$b = n - a - p_s q_s q_l f \frac{m}{s_0}$$

not depending on q_s (*b* was the number of wild-born individuals that were not descendants of adults breeding in the wild for the first time). Solving

$$\tilde{n} = a + p_s \tilde{q}_s q_l f \frac{m}{s_0} + b = m$$

yielded

$$\tilde{q}_s = \frac{s_0}{p_s q_l f} \frac{m - n}{m} + q_s \qquad (4)$$

for the value of q_s, corresponding to p_s or p_l on the isocline I_t, the right-hand expression being in fact independent of q_s.

ALGORITHM FOR COMPUTING RELEASE ISOCLINES

Life-cycle parameters of the species and release parameters were given as inputs. We chose a number $T > t_r$ of time steps (say $T = 30$) and a large number (say $N = 1000$) of values of $p = p_l$ or $p = p_s$ regularly spaced between 0 and 1. The algorithm is made of two nested loops.

For $b = 0$ to N, $p = b/N$; for $t = 1$ to T, we computed population sizes n and m and number a of introduced adults using matrix models 1 and 2; we computed $\tilde{q}$ according to equation 3 or equation 4; and we plotted point $(p, \tilde{q})$. At the end of the procedure the family $\{I_t; t = 1, ..., T\}$ of isoclines was obtained.