Research

Breeding habitat selection behaviors in heterogeneous environments: implications for modeling reintroduction

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Animal movement and habitat selection behavior are important considerations in ecology, and remain a major issue for successful animal reintroductions. However, simple rules are often used to model movement or focus only on intrinsic environmental cues, neglecting recent insights in behavioral ecology on habitat selection processes. In particular, social information has been proposed as a widespread source of information for habitat evaluation. We investigated the role of explicit breeding habitat selection strategies on the establishment pattern of reintroduced populations and their persistence. We considered local movement at the scale of a single population. We constructed a spatially-implicit demographic model that considered five breeding habitat selection rules: 1) random, 2) intrinsic habitat quality, 3) avoidance of conspecifics, 4) presence of conspecifics and 5) reproductive success of conspecifics. The impact of breeding habitat selection was examined for different release methods under various levels of environmental heterogeneity levels, for both long and short-lived monogamous species. When heterogeneity between intrinsic habitat patch qualities is high, the persistence of reintroduced populations strongly depends on habitat selection strategies. Strategies based on intrinsic quality and conspecific reproductive success lead to a lower reintroduction failure risk than random, conspecific presence or avoidance-based strategies. Conspecific presence or avoidance-based strategies may aggregate individuals in suboptimal habitats. The release of adults seems to be more efficient independent of habitat selection strategy. We emphasize the crucial role of oriented habitat selection behavior and non ideal habitat selection in movement modeling, particularly for reintroduction.

Reintroduction biology still faces a lack of theoretical underpinnings and suffers from high uncertainty in its management outcomes (Sarrazin and Barbault 1996, Armstrong and Seddon 2008). In this context, projecting how released individuals will use their new environment is a major challenge for reintroduction settlement and long term establishment (Cramer and Portier 2001, Bar-David et al. 2005). Simultaneously, most research on animal movement is "restricted within isolated sub-disciplines focusing on single phenomena" (Mueller and Fagan 2008), while uncertainty about dispersal function parameters often amplifies uncertainty in population viability analysis (PVA) predictions (Pulliam and Danielson 1991, Sutherland and Norris 2002). Broadly understanding settlement patterns within the framework of behavioral ecology can play a key role in future reintroduction planning and animal movement models. Indeed, an increasing number of behavioral studies have shown that individuals may obtain complex information on the distribution (Muller et al. 1997) or quality (Boulinier and Danchin 1997) of breeding habitat through social information, e.g. the presence or even the reproductive success of conspecifics (Valone and Templeton 2002, Danchin et al.

2004). Surprisingly, even though many studies have highlighted the need for more realism in modeling condition-dependent movement (South 1999, Cramer and Portier 2001, Gardner and Gustafson 2004), dispersal is often modeled as random walk, diffusion or simple transfer functions (Travis and French 2000, Bowler and Benton 2005). Only a few studies proposed to formalize social cues as conditions initiating movement decisions and settlement (Ray and Gilpin 1991, Doligez et al. 2003, Fletcher Jr. 2006). However, these studies investigated dispersal behavior for natural populations and mainly at the metapopulation scale, whereas reintroductions generally aim to re-establish one population in a target release site (i.e. at a local scale) where the species has completely disappeared. In addition, even if some studies have highlighted that animal decisions may be a misleading driver of habitat selection (Delibes et al. 2001, Kristan 2003) many others have often assumed that individual habitat selection results in optimal choices and distributions (e.g. the ideal free distribution, Fretwell and Lucas Jr. 1970, or the marginal value theorem, Charnov 1976).

 Here, we present a modeling study which investigates the consequences of post-release habitat selection behavior on

population viability in a reintroduction context. Indeed, during the settlement phase, released individuals have to settle in an unknown environment with limited information, due to the absence of conspecifics. In our study, inexperienced individuals have to select a habitat under both demographic and environmental stochasticies, which might entail the possibility of suboptimal habitat choices. The viability of the reintroduced population was evaluated at a 'local' population scale under various habitat selection strategies, species life-cycles, heterogeneous environmental conditions and release methods. On the other hand, we modeled movement in agreement with Mueller and Fagan (2008), who advocated the use of three classes of movement mechanisms to provide a comprehensive framework for complex animal movement. We thus considered a) a non-oriented or random mechanism, at least for the first year after release when information on habitat quality was not available, b) an oriented mechanism relying on perceptual cues such as conspecifics or intrinsic habitat quality, and c) a memory-based mechanism across the use of private information. Such a movement framework could greatly improve the understanding of settlement processes and the reliability of reintroduction modeling.

Methods

Habitat quality and breeding sites

The environment consisted of three distinct breeding habitat patches. These habitat patches, which occur at the scale of a local population constituted the subunits of a single reintroduction target area (Fig. 1). For semantic clarity, when we referred to the 'local' population in this paper we followed the definition of Baguette and Stevens (2003), in which local scale was determined by "the relationship between the mean mating probability of an

individual with a given conspecific and distance". Thus we only considered local movements resulting from habitat selection behavior within this local population, i.e. from one breeding patch to another (Bowler and Benton 2005) rather than dispersal between different populations. Therefore, distance was not explicitly depicted and movements per se were assumed not to affect fitness, as it is traditionally the case in ideal free and ideal despotic distribution models (Fretwell and Lucas Jr. 1970, Johnson 2007). Each habitat patch i was characterized by an initial habitat quality index $q_{i,0}$ at time $t = 0$ and a limited number of 30 identical breeding sites, yielding a total carrying capacity of 90 breeding sites. The breeding site was considered to be an exclusive breeding place for one pair. Since our model was spatially implicit, this site could reflect a breeding territory as well as a breeding place for colonial species. Since we focused on the population establishment phase, we assumed no negative density-dependence in demographic parameters and the number of breeding sites was the only limit on population growth. Indeed, density dependent feedback would be important only for large population sizes, i.e. when the reintroduction was successful. The carrying capacity was arbitrarily chosen; however, increasing the carrying capacity would certainly not change extinction probabilities since we did not model catastrophic events. Thus, extinction should occur well before the reintroduced population reached the carrying capacity of 90 breeding pairs.

Habitat quality of patch i at time t ($q_{i,t}$) was assumed to only affect reproduction. Indeed, we considered mobile species, and individuals could easily explore the overall reintroduction area without costly movements. Except for breeding sites, individuals shared the same environment and had equal access to other resources. The patch quality varied over time and was autocorrelated between consecutive years following:

$$q_{i,t+1} = AC \times (q_{i,t} - q_{i,0}) + \beta (q_{i,0}, \sigma)$$

where AC was the temporal autocorrelation coefficient, $\beta(q_{i,0}, \sigma)$ a beta function with mean $q_{i,0}$, and variance $\sigma = 0.15\sqrt{(1 - AC^2)}$. The environment could be either highly predictable (AC = 0.8) or unpredictable (AC = 0) (Doligez et al. 2003). We defined eight scenarios of heterogeneous environmental conditions, S1 to S8, according to differences in initial quality among patches and temporal autocorrelation (Table 1). Two kinds of environmental stochasticity could be distinguished within these scenarios: a 'local' stochasticity (S1 to S4), in which each patch was affected independently from the others but with the same variance, and a 'global' stochasticity (S5 to S8), in which the three patches were affected by the same environmental variation each time step. Local stochasticity mimicked habitat subunits of equal quality encountering different perturbation regimes independently, whereas global stochasticity corresponded to intrinsically distinct habitat quality subunits under the same environmental variations.
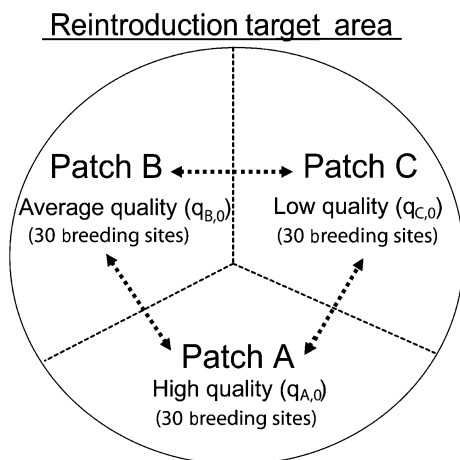

Figure 1. Representation, at the population scale, of the available heterogeneous environment constituting the entire reintroduction target area of 90 breeding sites. Habitat patches had an intrinsic initial quality $q_{A,0}$, $q_{B,0}$, $q_{C,0}$ affecting reproduction success (Table 1) and contained 30 breeding sites each. The reintroduction target area was composed of these three distinct habitat patch subunits A, B, and C. Dotted arrows indicate possible between-patch movements by breeding pairs from time t to t+1.

Table 1. Heterogeneous environmental scenarios examined in the model. Local stochasticity, temporal variation in quality, was independent among patches. Global stochasticity was represented by stochastic events that affected the habitat qualities of the three patches in the same way.

Environmental stochasticity	Intrinsic habitat characteristic	Initial quality $q_{i,0}$*			Temporal autocorrelation coefficient (AC)	Scenario
		High	Average	Low		
		Patch A $q_{A,0}$	Patch B $q_{B,0}$	Patch C $<l_{C,0}$		
Local	Homogeneous	1	1	1	0	S1 S2
					0.8	
	Moderately heterogeneous	1	0.85	0.7	0	S3 S4
					0.8	
Global	Moderately heterogeneous	1	0.85	0.7	0	S5 S6
					0.8	
	Extremely heterogeneous	1	0.5	0.15	0	S7 S8
					0.8	

*Each breeding habitat patch A, B and C is characterized by an initial intrinsic quality $q_{i,0}$ that varied in nest success probability with autocorrelated stochastic events.

Population modeling

We used age-structured models (Caswell 2001) to study the dynamics of reintroduced populations (Sarrazin and Legendre 2000). Our model described the age-structured female life cycle of species with birth pulse reproduction and a pre-breeding census. A one year time step was used, with a single annual breeding event. The model integrated demographic stochasticity on survival (binomial functions of survival probabilities given in Table 2) and fecundity (details below), and environmental stochasticity on habitat quality ($q_{i,t+1}$). Breeder's patch allocations resulted from stochastic processes as well, since habitat selection was achieved through binomial functions in which breeders had strategy-specific patch selection probabilities (Table 3).

Two different life cycles were considered in order to examine reintroduction cases of species with contrasted life history traits. Long-lived and short lived species (hereafter LLS and SLS, respectively) were modeled using demographic parameters available for two bird species (Table 2):

Table 2. Demographic parameters used in the models for the long-lived species (LLS and LLS*) and for the short-lived species (SLS), taken from the griffon vulture (Sarrazin et al. 1994, 1996) and the barn swallow (Møller 1994), respectively.

Demographic parameter	Life cycle		
	Long-lived		Short-lived
	(LLS)	(LLS*)	(SLS)
Adult survival rate (sa)	0.987	0.937	0.45
Juvenile survival rate (sj)	0.858	0.815	0.3
Fecundity (f)	0.8	0.8	8
Adult survival with release cost	0.74[a]	0.74[a]	0.34[a]
Adult fecundity with release cost	0.51[a]	0.51[a]	4.08[a]
Sex ratio	0.5	0.5	0.5
Age at first breeding (in year)	4	4	1
Proportion of breeders (a)	0.8	0.8	0.8

[a]Release cost on survival was estimated from a reintroduced population of griffon vulture and applied to the barn swallow. Adult survival and fecundity with release cost have been calculated as sa(1−cs) for survival and as f(1−cf) for fecundity, with cost on survival (cs) =0.25 and cost on fecundity (cf) =0.49 (see also Sarrazin et al. 1994, 1996).

the short-lived barn swallow *Hirundo rustica* and the long-lived griffon vulture *Gyps fulvus* (Sarrazin and Legendre 2000, Doligez et al. 2003, Robert et al. 2004). However, since LLS survival rates were particularly high, we also performed simulations with a 5% reduction in griffon vulture survival rates to extend the generality of our approach. In this case, all other parameters were equal to those of the LLS and consequently all the simulations using these reduced survival rates are hereafter denoted as LLS* (Table 2). Importantly, while we selected birds as model animals to formalize our generic structured model, demographic parameters from any other organisms could also have been used.

We assumed that released individuals could reproduce the year of their release, but suffered demographic release costs (i.e. decreased fecundity and survival; Sarrazin and Legendre 2000) due to captivity or stress (Beck et al. 1994). Costs were expected to be higher for adults than for juveniles due to long captivity and stressful release methods, for long-lived and short-lived species respectively. We used released adult costs for survival (cs) and for fecundity (cf) estimated by Sarrazin et al. (1994, 1996), for both life cycles (Table 2). The survival cost acted only during the first year after release, whereas the fertility of introduced individuals was decreased throughout the entire lifespan (Sarrazin and Legendre 2000). Release costs were not heritable.

Following Sarrazin and Legendre (2000), we assumed the proportion of potential breeders to be $\alpha = 0.8$, which included first time breeders and surviving individuals that were mature during the previous year. Fecundity was independent of population size in our study and breeding success varied only with the intrinsic habitat patch quality ($q_{i,t}$; Table 1). For LLS, the number of offspring produced was given by a binomial function of mean $f_{i,t}$ in habitat patch i at t such as:

$$f_{i,t} = f \times q_{i,t}$$

with f being the fixed mean fecundity (Table 2). The annual number of successful breeding sites was equal to the number of offspring produced, since LLS breeders can have at most one offspring per year (Table 2). For SLS, the habitat patch quality $q_{i,t}$ gave the number of successful breeding pairs

Table 3. Definition of the five breeding habitat selection strategies and patch selection probabilities, depending on reproductive status (either breeders or first time breeders and non- breeders).

Habitat selection strategy	Definition	Dispersal probability dp $_{i,t+1}$*	
		Emigrating breeders	First time breeders and previous non-breeders
Random (R)	Random distribution, breeders settle with the same probability in all reproductive patches between time t and t+1	1/2	1/3
Quality (Q)	Breeders choose the reproductive patch i at time t+1 according to the relative intrinsic environmental quality of the reproductive patch i at time t	$\dfrac{q_{i,t}}{\Sigma_{j\in J}q_{i,t}}$	$\dfrac{q_{i,t}}{\Sigma_{k\in K}q_{i,t}}$
Avoidance (A)	Breeders choose the reproductive patch i at time t+1 according to the lower relative number of conspecific breeders in patch i at time t	$1-\dfrac{nr_{i,t}}{\Sigma_{j\in J}nr_{j,t}}$	$1-\dfrac{nr_{i,t}}{\Sigma_{k\in K}nr_{k,t}}$
Presence (P)	Breeders choose their reproductive patch i at time t+1 according to the relative number of conspecific breeders in patch i at time t	$\dfrac{nr_{i,t}}{\Sigma_{j\in J}nr_{j,t}}$	$1-\dfrac{nr_{i,t}}{\Sigma_{k\in K}nr_{k,t}}$
Success (S)	Breeders select their reproductive patch i at time t+1 according to the relative conspecific reproductive success in patch i at time t	$\dfrac{sr_{i,t}}{\Sigma_{j\in J}sr_{j,t}}$	$\dfrac{sr_{i,t}}{\Sigma_{k\in K}sr_{k,t}}$

*The probability to select to the patch i at t+1 was based on criteria at time t, where $q_{i,t}$ = intrinsic environmental habitat quality of patch i at time t, $nr_{i,t}$ = number of conspecific breeders in patch i at time t, $sr_{i,t}$ = reproductive success rate of conspecifics in patch i at time t, J = the two available patches after the decision to leave the current one, and K = the three patches forming the total environment.

producing at least one fledgling. The total number of fledglings per successful pair was given by a Poisson function with mean fecundity f (Table 2). Reproductive success was calculated as the mean number of offspring per breeding pair for both life cycles.

Breeding habitat selection strategies

Following Armstrong et al. (2005), we distinguished first year versus older breeders, and allowed breeders to move among patches after each breeding event. Breeders seem to refer preferentially to their own reproductive experience – personal or private information – to select their breeding patch (Valone and Giraldeau 1993, Citta and Lindberg 2007). They can thus decide to stay or leave according to their private information (Boulinier and Danchin 1997). We explicitly included private information behavior in each habitat selection strategy: after each breeding event, breeders first chose to stay or leave according to their private information; in a second step, breeders that chose to leave (i.e. emigrating breeders) selected a new habitat patch for the next year similarly to non-breeders (Table 3). To simulate private information for LLS, we derived mean pair fidelity estimates from a long-term study of a reintroduced population of griffon vulture in the Grands Causses, France (Le Gouar unpubl.). In this case, successful LLS breeders stayed in their breeding patches with a rate of 0.918, whereas unsuccessful breeders stayed with a rate of 0.801. In the absence of data for the barn swallow, we used the territory fidelity rates estimated from another passerine species, the willow flycatcher *Empidonax traillii* for SLS simulations, and determined fidelity rates of 0.814 and 0.6, for successful and unsuccessful breeders respectively (Sedgwick 2004). As these parameters assumed strong specific fidelity, even for unsuccessful breeders, we also tested the robustness of these results with the more classic fidelity rule

"win stay, lose shift" (Frean 1994). In this case, the probability of staying was 1 for successful reproduction and 0 for failed reproduction, whatever the habitat selection strategy.

Five breeding habitat selection strategies were specified for between patch movements, each differing in the cues used by the individuals to select the breeding patch: 1) random movement (hereafter Random) versus movements based on 2) intrinsic habitat patch quality (Quality) in which habitat choice was determined by an optimal assessment of environmental cues, 3) conspecific avoidance (Avoidance) to mimic a disturbance to settle near conspecific, 4) attraction to the presence of conspecifics (Presence) and 5) attraction to high conspecific reproductive success (Success). Strategies Presence and Success thus mimicked habitat selection through two kinds of social cues (Table 3). As commonly reported, habitat selection was based on previous breeding season criteria (Reed and Dobson 1993, Doligez et al. 2003). The probability to select a breeding patch i at t+1 to breed (dp$_{i,t+1}$) depended on the habitat selection strategy and was calculated at time t among the three habitat patches for first time breeders and non-breeders (no private information), and among two habitat patches after leaving the current one for emigrating breeders (Table 3). Potential breeders of each class had the same probability of selecting a patch and were able to select a new habitat patch after every year during their entire lifespan, i.e. not only after the year of release. Breeders were allocated to patch i through a binomial function of mean dp$_{i,t+1}$ (Table 3). If a patch was full, breeders could settle in the second preferred patch according to the strategy if there were still enough places, and so on. Patch allocation concerned breeders only. In fact, while contributing to the population size, non-breeders could be considered as floaters inhabiting the reintroduction area. At the beginning of each simulation, no habitat selection information was available
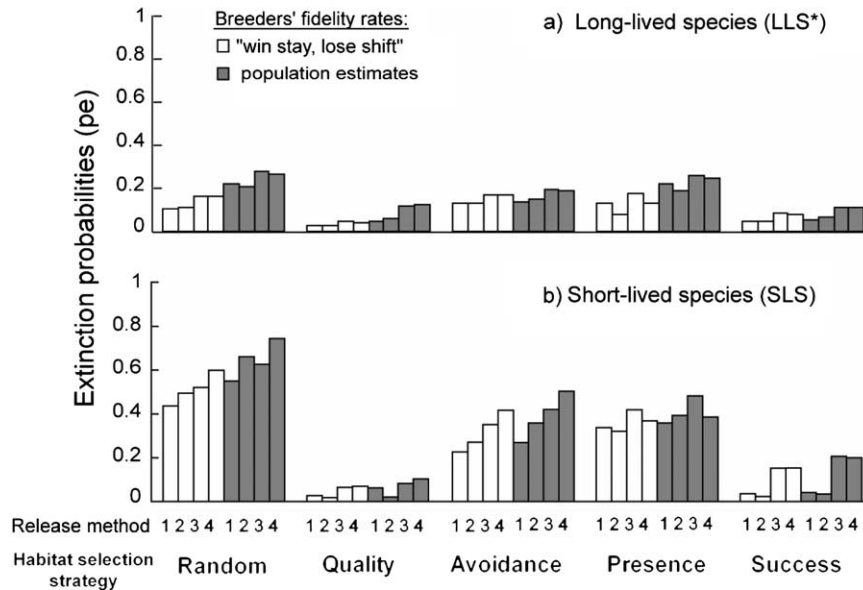
Figure 2. Extinction probabilities of the short-lived (SLS) and the long-lived (LLS*) species reintroduced population for two different fidelity rates. We considered the release of 20 individuals under four release methods: 1) 20 adults during 1 year; 2) 2 adults per year during 10 years; 3) 20 juveniles during 1 year; 4) 2 juveniles per year during 10 years. Five breeding habitat selection strategies were considered (Table 3). Fidelity rates: the 'win stay, lose shift' rule (white) compared to fidelity rates estimated from a reintroduced population of griffon vulture for LLS* and from a population of willow flycatchers for SLS (grey). Figure plots the results based on 1000 Monte Carlo simulations during 10 generations resulting of the age-structured female life cycle demographic model, under global environmental stochasticity in an extremely heterogenous habitat (scenario S7; similar results for scenario S8).

for released individuals, i.e. neither conspecific information nor private information. Habitat selection was then random among the three patches, to mimic the uncertainty in patch selection for inexperienced and uninformed animals, typical of a reintroduction context.

Release method scenarios

We considered two components of the release methods: age of released females, adult versus juvenile, and duration of release. For each environmental scenario, breeding patch selection strategy and life cycle, we modeled the release of 20 females under four modalities: 20 females in a single release or two females per year over ten years, for both adults and juveniles. Since our model considered monogamous species through a female life cycle, it meant that the 20 released females represented 20 potential breeding pairs, assuming a 1:1 sex-ratio and that all released females may mate. Therefore, results were expected to be slightly optimistic (Legendre et al. 1999). Our simulations should then be interpreted as the release of 40 individuals since males were implicitly considered and population size was expressed as the number of females. We chose the number of released individuals as a compromise between the small numbers of individuals released for LLS and the large number of individuals used for SLS reintroductions (Griffith et al. 1989).

Model simulations

We used the ULM software (Legendre and Clobert 1995), which is a powerful tool to compute structured population models based on species life cycles in a general framework of

discrete dynamical systems (Caswell 2001). Each simulation was computed through Monte Carlo simulations of 1000 population trajectories over 50 years. However, this time scale can entail very different issues for long and short-lived species. We therefore considered a time horizon of 10 generations after release when comparing the effect of the habitat selection strategies on the extinction probabilities between life cycles. We used matrix models to calculate the mean generation length (Caswell 2001) with the demographic parameters given in Table 2, which were 1.46 years for SLS, 10.96 for LLS and 10.95 for LLS*. Simulating reintroductions, there were no individuals in the habitat before release. Population viability was assessed through the population extinction probability (pe), where extinction is defined as zero population size across the entire reintroduction area.

We did not use formal statistical tests to compare projected extinction probabilities among our different scenarios. Modeling outcomes, contrary to empirical data, are the result of different hypotheses inherent to the model structure and the scenario investigated. Thus, quantitative results remain, by definition, intrinsically different among these scenarios. However, projected extinction probabilities allowed us to assess the direction and magnitude of differences among scenarios. The mean population size and the reproductive success of the population were calculated from all non-extinct trajectories. We also defined the aggregation coefficient (Ag) as the ratio of the variance in the total number of breeding pairs between the three patches to the average number of breeding pairs per patch:

$$Ag = \sum (nr_i - nr_m)^2 / nrm$$

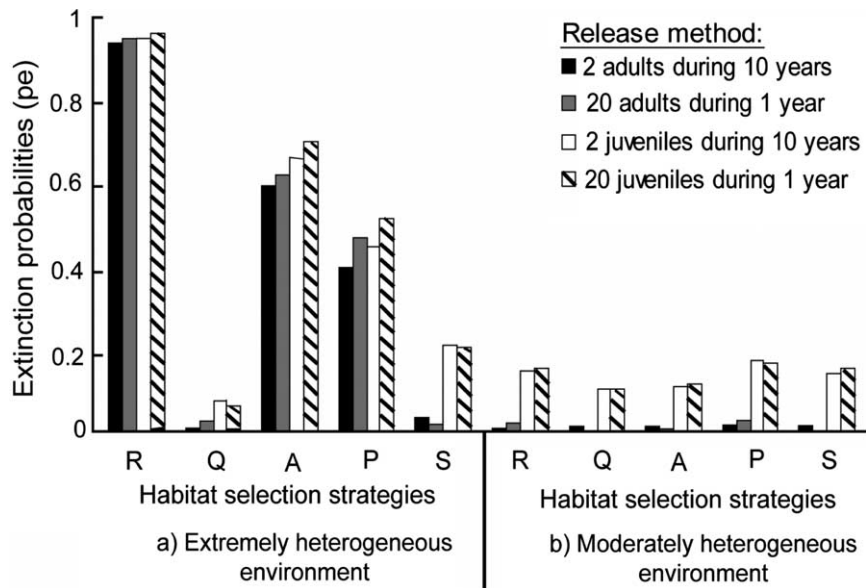with nr_i the number of breeders in patch i, nr_m the mean

Figure 3. Extinction probabilities of a reintroduced population of a short-lived species according to breeding habitat selection strategies and release methods under two scenarios of environmental heterogeneity. We considered the release of 20 individuals under four release methods, for five habitat selection strategies (Table 3) within 1000 runs Monte Carlo simulations of the age-structured female life cycle demographic model for 50 years. Two scenarios of 'global' environmental stochasticity were considered: a) extreme (scenario S7) and b) moderate (scenario S6).

number of breeders among patches. This coefficient measures the dispersion of a Poisson-like probability distribution (with values higher than 1 indicating aggregation), and is often used in experimental studies to measure the clustering degree (Lancaster et al. 2003).

Results

Breeding habitat selection strategy and extinction probabilities

Habitat selection behavior influenced extinctions of both SLS and LLS* over 10 generations, mainly in an extremely heterogeneous environment under global environmental stochasticity (Fig. 2). The two life-cycles showed comparable responses to habitat selection strategies: the Quality and Success strategies had the lowest extinction risk when the environment was extremely heterogeneous. Presence, Avoidance and Random strategies yielded much higher risks, with extinction probabilities reaching 0.27, 0.22 and 0.33 respectively for LLS*, and 0.48, 0.50 and 0.75 respectively for SLS. In contrast, there was no extinction of the reintroduced population for the LLS after 10 generations whatever the breeding habitat selection strategy. When considering extinction probabilities over 50 years under global stochasticity, the strong effect of the habitat selection strategy on population persistence was confirmed for SLS (Fig. 3). In contrast to the extremely heterogeneous habitat scenario (Fig. 3a), all strategies yielded similar extinction probabilities within a given release method under a moderately heterogeneous habitat (Fig. 3b). The LLS* extinction probabilities were very low under moderate habitat heterogeneity and did not allow to distinguish between the effects of strategies and benefits of the release methods.

Effect of the different breeder's fidelity rates

Extinction probabilities for LLS* and SLS over 10 generations varied little between scenarios that used estimated fidelity probabilities versus the 'win stay, lose shift' rule, although the former were more pessimistic (i.e. higher extinction; Fig. 2). Thus our inferences of the effects of habitat selection on extinction probabilities proved robust. We found no difference in the reintroduction viability between the two fidelity rules, as well as for population size and breeding success for LLS.

Environmental stochasticity

Local stochasticity and environmental predictability
Under localized environmental stochasticity (scenarios S1–S4), the predictability of environmental quality across years had little or even no effect in both life cycles, whatever the habitat selection strategy. Similarly, breeding habitat selection strategies did not influence population size, extinction probability or mean reproductive success, but affected the distribution of breeding pairs: Presence and Success strategies were aggregative strategies (Ag >1, Fig. 4) whereas Quality and Random strategies yielded random distributions (Ag 1, Fig. 4). We also detected a progressive decrease in Ag due to the spread of breeders across all patches after about 10 or 20 years (for SLS and LLS, respectively).

Global stochasticity
Under global stochasticity (scenarios S5–S8), differences between strategies were more perceptible. The Success and Quality strategies led to the highest population size and reproductive success for both life cycles, followed by Presence, Avoidance and Random respectively (Fig. 5). In addition to the Success and Presence strategies, the Quality
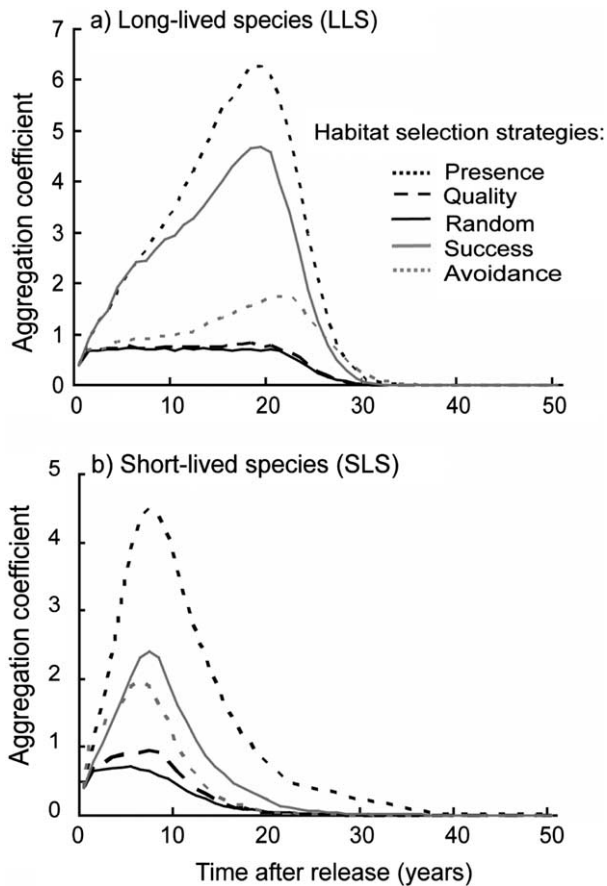
Figure 4. Aggregation coefficient of breeding pairs (Ag) among three breeding patches according to habitat selection strategies in a moderately heterogeneous environment under local stochasticity, for both long and short-lived life cycles. Ag was the ratio of the variance in the total number of breeding pairs between the three habitat patches to the average number of breeding pairs per patch. Monte Carlo simulations and habitat selection strategies similar to Fig. 3 under the environmental scenario S4 (similar results with scenarios S1 to S3) for a single release of 20 adults. (Ag > 1: aggregated distribution; Ag = 1: random distribution; Ag < 1: homogeneous distribution of breeders).

strategy was also aggregative under global stochasticity (Fig. 5a–b). This aggregation was maintained over time in the SLS (Fig. 5b), whereas breeders were homogeneously spread 50 years after release in LLS due to the saturation of breeding sites (Fig. 5a). The aggregation coefficient and reproductive success for LLS* showed a 20 year delay with comparable patterns and values to those of LLS.

Short-term reproductive success and population size were closely related to distribution patterns, particularly for SLS. After 50 years, the reproductive success in each habitat selection strategy converged, except for Random in SLS (Fig. 5d). The entire population sizes did not reach equilibrium under any scenarios for LLS (Fig. 5e), while all the breeding sites were occupied (Fig. 6a, 6c). Interestingly, population sizes of LLS* after 10 generations were narrowed in the same way as those obtained for SLS (Fig. 5f).

In contrast to local stochasticity which generated independent variations among patch qualities, global stochasticity led to constant variations between patch qualities and yielded lasting differences in patch occupancy

depending on selection strategies. Patches A and B, the two higher habitat quality patches, were more populated than patch C for the Success and Quality strategies (Fig. 6a–b). For the Random strategy, breeding pairs were equally distributed among the three areas (Fig. 6c–d). Unlike for LLS, the number of breeding pairs for SLS, widely depended on the habitat selection strategies (Fig. 6).

Presence strategy showed intermediate trends in distribution between patches, whereas a strong aggregation of breeding pairs occurred for Presence (Fig. 5a–b). In fact, for each trajectory, breeding pairs with the Presence strategy were aggregated in a given patch, which differed across the 1000 implemented trajectories, yielding no detectable preference for a given patch across all simulations. In contrast, the Success and Quality strategies always led to aggregation into the highest quality patch.

Release method scenarios

For SLS, the release of adults might reduce the risk of extinction depending on environmental heterogeneity and habitat selection (Fig. 2). For example, with high environmental heterogeneity (scenarios S7 and S8) extinction probabilities of the Success strategy were low when releasing adults and much higher when releasing juveniles (e.g. pe = 0.08 and 0.22, respectively, in Fig. 3a). This trend was less detectable with other strategies: scenarios S1 to S6 yielded comparable results and releasing adults was always better (Fig. 3b). Sequential release had minor effects on population viability and reintroduction success since these factors benefited from non-delayed release only in the Presence strategy in a very heterogeneous landscape. For LLS and LLS*, differences between the effects of releasing adults versus juveniles were small. Releasing adults produced slower growth rates than releasing juveniles, due to the long-term effects of reproductive cost for these species. Despite the fact that the low extinction probabilities prevented clear conclusions for LLS*, adult releases tended to induce the same benefits as those obtained for SLS.

Discussion

Breeding habitat selection strategies affect short term reintroduction success

Habitat selection strategies strongly affected reintroduced population establishment pattern and short term viability for both short and long-lived species when survival were reduced (LLS*), especially under conditions of high environmental heterogeneity (Fig. 5). Aggregation occurred for strategies based on social cues regardless of environmental conditions (Fig. 4, 5a–b), corroborating previous studies on colonization processes and habitat selection through conspecific copying (Danchin et al. 2004, Citta and Lindberg 2007). This unequal distribution of breeding pairs into different quality patches (Fig. 6) may affect population viability (Fig. 5). Strategies using a 'habitat performance index', via assessment of intrinsic habitat quality or conspecifics reproductive success, induced aggregation into optimal breeding patches. In contrast, conspecific attraction and avoidance sometimes produced aggregation in suboptimal
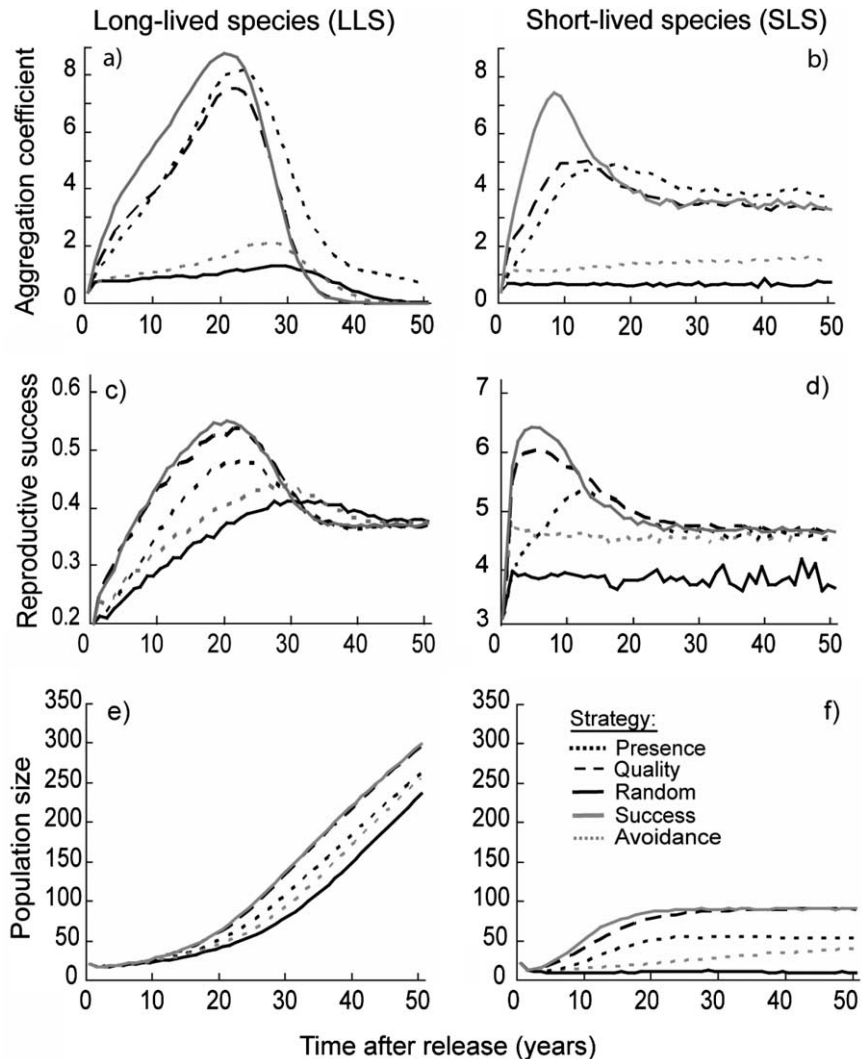
Figure 5. Effect of five breeding habitat selection strategies in an extremely heterogeneous environment on the aggregation of breeding pairs, the reproductive success and the size of the reintroduced population, for two life cycles: long-lived (a, c and e) and short-lived life cycle (b, d and f). The reproductive success was the number of young per breeding pairs and the population size reflected the number of females in our female life cycle demographic model. Aggregation coefficient Ag: Ag > 1 indicates an aggregated distribution; Ag = 1, a random distribution; Ag < 1, a relatively homogeneous distribution of breeders. Simulations and habitat selection strategies similar to Fig. 3a.

habitats, either by leading animals to select poor and avoid rich habitats (Railsback et al. 2003) or by compelling subordinate individuals to settle in poor habitats (Serrano and Tella 2007). On the other hand, breeders with random dispersal try to breed wherever they can. As such, Avoidance, Random and Presence strategies appeared to be detrimental as compared to Success or Quality strategies under the same environmental conditions (Fig. 2, 3). Our results therefore confirmed that habitat quality should not be assessed and modelled as a function of resource availability only. Rather, external factors that may affect habitat choice, such as conspecific presence or success, should also be included. We thus recommend gathering additional information about the habitat selection strategy of the target species during the preparatory phase of reintroduction.

Extinction probabilities in a heterogeneous breeding habitat for the two life cycles were consistent with previous conclusions. For LLS, we observed a low sensitivity of

population viability to variation in reproduction parameters (Sarrazin 1998, Schaub et al. 2004), whereas SLS expressed a high sensitivity to reproduction (Legendre et al. 1999). However, a 5% reduction in LLS survival rates (LLS*) was sufficient to highlight that breeding habitat selection strategies might also be of great concern for long-lived, endangered species. Interestingly, LLS* simulations highlighted the problem of time horizon at which the success of reintroduction should be defined. Such time scales may then encompass the viability of the population from the establishment phase after animal releases to the sustainability of the growing and regulation phases.

Temporal autocorrelation

Surprisingly, we detected no effect of temporal autocorrelation in the habitat quality for any life cycle. Indeed, extinction probabilities did not differ more than 0.005

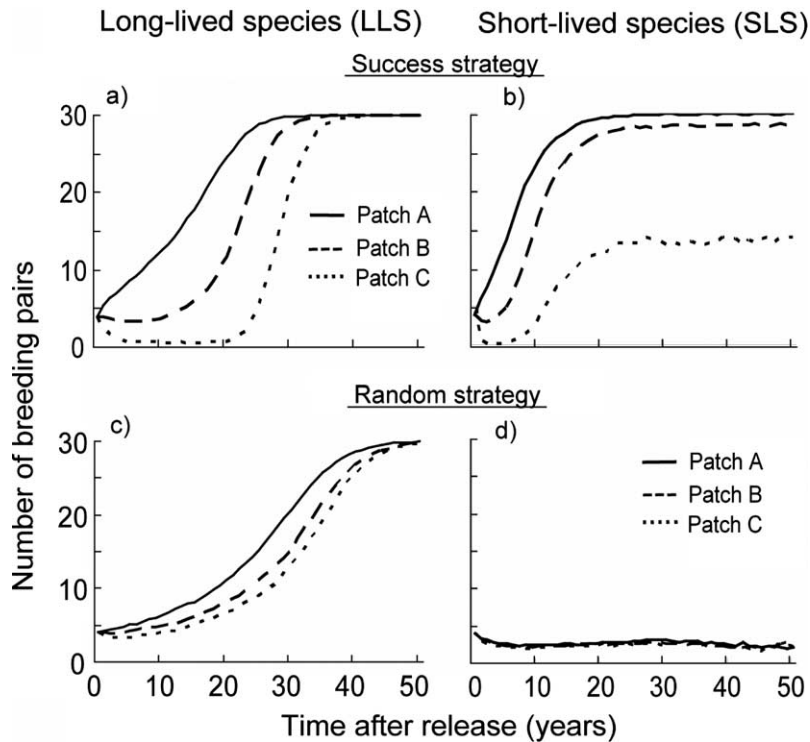Long-lived species (LLS) Short-lived species (SLS)

Figure 6. Distribution of breeding pairs among the three habitat patches according to two different habitat selection strategies in an extremely heterogeneous environment for both life cycles. Simulations as described in Fig. 5.

between AC = 0 and AC = 0.8 for scenario S1 to S8. We expected that the predictability of the environment would result in differences in population persistence and dynamics, at least for the local stochasticity scenario where the patch quality rank varied across time (i.e. between S1 and S2, and between S3 and S4). Indeed, studies investigating the consequences of habitat selection strategies based on cues available the previous year (Doligez et al. 2003) or site fidelity rates (Schmidt 2004) underlined the sensitivity of long-term animal population persistence to the predictability of environmental quality. However, we did not compute simulation times comparable to those studies. Instead, we investigated shorter management time scales rather than evolutionary consequences. Additionally, according to Schmidt (2004), the mean persistence time of a network of three patches (as was the case in our study) remained in agreement with our results (about 160 and 200 years for AC = 0 and AC = 0.7 respectively). Finally, in the context of strong global changes, further analyses considering increasing variances in habitat quality and temporal autocorrelation may lead to very interesting complementary results.

Specific effects of release method

For SLS, the age of released individuals impacted reintroduction success regardless of habitat selection strategies and habitat heterogeneity. Releasing adults considerably reduced extinction probabilities for all habitat selection strategies and generally appeared less risky than releasing juveniles (Fig. 3). In fact, reintroduced adults suffering from

reproductive cost quickly disappeared and did not cause a long-term reproductive reduction in the population. In contrast, both single and sequential releases seemed to have no consequences for the reintroduced population, whatever the life cycle.

The benefits from any of the release methods were more difficult to prove conclusively for long-lived species. Using a strict demographic modeling approach, Sarrazin and Legendre (2000) concluded that in long lived species, the release of adults could be more effective, mainly because of their higher reproductive value. However, integrating genetic effects, Robert et al. (2004) found that the releases of juveniles might have subsequent positive consequences for long-term persistence. In our study, we could not clearly distinguish the advantages of any release method nor could we confirm these previous conclusions for long lived species. In fact, although the LLS* simulations could indicate a slight advantage of releasing adults in term of extinction risks (Fig. 2), releases of juveniles induced long-term benefits in terms of population growth among extant trajectories (not shown). These long-term benefits could be mainly explained by the cost to fecundity of released adult individuals, which was assumed to act during the entire lifespan and, consequently persisted over a long time interval for LLS. Old released adults occupied the best breeding sites with the advantage of their personal breeding experience, compelling juveniles to breed in poorer sites. This finding emphasizes that the use of social cues, which can lead to the unequal distribution of individuals among habitats, can be compatible with the Ideal despotic distribution theory and observed despotic behavior (Serrano and Tella 2007). Most importantly, due to the dichotomy

between establishment and persistence phases in reintroductions (Armstrong and Seddon 2008), "reintroduced populations can fail to survive the establishment phase in conditions that would enable long-term persistence". Thus, release methods could benefit to one of these phases but not necessary to both.

Perspectives for integrating dispersal behavior in population modeling

Referring to the recurrent problems associated with the estimation of dispersal in spatially-explicit population models (SEPM) and their weakly reliable guidance for conservation (Ruckelshaus et al. 1997), Wiegand et al. (2004) stated that there were low sensitivities and strong robustness of SEPMs against dispersal uncertainty. In this case, these authors studied the reintroduction the brown bear *Ursus arctos*, a long lived species, in Austria. Although our model was not spatially-explicit, our results confirmed that dispersal and habitat selection behavior can weakly affect the dynamics of long-lived species in heterogeneous landscapes if there is no cost associated with movements. However, we additionally considered short-lived species or a slight reduction in long lived species for which habitat selection strategies may have a strong impact on population viability. Indeed, we underline that care should be taken for short-lived species as well as for endangered long-lived species facing decreased survival, especially when species use conspecific cues to select their breeding habitat.

Since no costs were associated with movement across our simulations, the results would not qualitatively change if space was explicitly modeled given a similar hypothesis. On the contrary, costs in crossing an unsuitable matrix in a spatially-explicit metapopulation model (with e.g. different size and isolation levels) might be associated with higher extinction probabilities. Indeed, searching and settlement cost through conspecific attraction behavior have been shown to strongly influence survival and fecundity (Fletcher Jr. 2006). However, Fletcher Jr. (2006) assumed that conspecifics correctly assess environmental quality, as it has been commonly hypothesized in the traditional distribution modeling by the "optimal theory" (Fretwell and Lucas Jr. 1970). Nevertheless, many causes may explain suboptimal animal distributions (Delibes et al. 2001, Kokko and Sutherland 2001, Arlt and Part 2007), including despotic behavior (Serrano and Tella 2007) or time lags and site fidelity (Davis and Stamps 2004). Here, we pointed out that species using conspecific attraction or avoiding their congeners sometimes lead to non ideal breeding habitat selection. We argued that, in heterogeneous environment, breeding habitat quality cannot be predicted accurately by the optimal theory's assumption only, confirming previous conclusions considering social foraging behavior (Hancock and Milner-Gulland 2006). However, we did not consider the case where poor habitats are preferred to high quality habitats such as in ecological trap (Kristan 2003), for which extinction risks would be higher than the Random strategy. Rather we preferentially consider a more general case of non ideal habitat selection to emphasize the problem of systematically assuming the optimal habitat selection in movement models. Mismatches between selection criteria and environmental quality also support the hypothesis that conspecific density could be a poor habitat quality indicator or even maladaptive (Doligez et al. 2003, Danchin et al. 2004). Such aggregative behavior could be seen as a possible indirect Allee effect, which is already known to depress growth rates of newly founded colonies, making many colonization events ephemeral (Veit and Lewis 1996).

Specific recommendations for reintroduction management

Reintroduction biology is widely concerned with habitat selection behaviors, from the effective settlement of released individuals in the reintroduction area to the use of this habitat by the animals. Indeed, few founders kept in captivity for a long time may show altered behavior or inexperience in the wild, and may consequently wrongly influence the site selection of subsequent breeders. We emphasize that, even if individuals do not escape from the reintroduction site, reintroduction success and population persistence greatly depend on the settlement pattern resulting from habitat selection behavior. Future studies integrating explicitly more realistic behavior in reintroduction program would help to adapt release methods to the behavioral patterns of target species. To a priori project reintroduction success and to assign appropriate adaptive management measures, we encourage reintroduction biologists to not only evaluate the habitat quality, defined as the real biological requirements of the species (Armstrong and Seddon 2008) but also to carefully investigate behavioral features such as movement, home range and habitat selection of free-ranging, wild-born individuals of the target species to be reintroduced (Kleiman 1989). Finally, we recommend to preferentially release adults rather than juveniles, and to create artificial social information for species cueing on conspecifics for settlement, e.g. by installing decoys or by keeping captive but visible conspecifics in the best habitat to promote its colonization. Researchers and managers must understand how temporal and spatial scales influence habitat selection behaviors and their demographic consequences during reintroduction, in order to properly estimate and model animal requirements.

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