



# When to use public information for breeding habitat selection? The role of environmental predictability and density dependence\*

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To select their future breeding site, individuals usually have to assess local quality by using environmental cues. One optimal cue may be 'public information', the local reproductive success of conspecifics in a breeding patch (patch reproductive success) because it integrates the effect of all environmental factors on breeding success. However, the quality of information conveyed by patch reproductive success is likely to depend on (1) environmental predictability and (2) interactions between individuals. We investigated how these two factors, ignored by previous models, affect the performance of individuals using patch reproductive success for breeding habitat selection compared with other information. We built a two-patch, game-theoretical model to compare the success of a strategy of breeding habitat selection based on patch reproductive success relative to four other strategies: (1) random patch choice; (2) philopatry; (3) choice based on the presence of conspecifics the previous year (conspecific attraction); and (4) choice based on intrinsic patch quality the previous year. The results illustrate how the efficiency of strategies in tracking variations in patch quality depend on environmental predictability and costs linked to density dependence, themselves linked to the dynamics of spatial aggregation of individuals. In particular, strategies based on measures of patch reproductive success perform the best for intermediate and high temporal predictability of patch quality, whereas philopatry and conspecific attraction then perform poorly. The 'conspecific attraction' strategy always coexists with other strategies by efficiently parasitizing the information they use. We discuss the implications of a better understanding of breeding habitat selection behaviours for evolutionary and conservation biology.

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Breeding habitat quality strongly influences the fitness of individuals through different environmental components, which may vary both spatially and temporally (Orians & Wittenberger 1991; Boulinier & Lemel 1996). Individuals are thus under strong selective pressures to make optimal breeding habitat choices. There is growing evidence that individuals are able to track variations in local breeding habitat quality (Klopfer & Ganzhorn 1985; Petit & Petit 1996; Reed et al. 1999), and empirical studies

have described many possible cues for breeding habitat selection. In most species, breeders rely on their own success to assess the quality of their current breeding patch and decide whether to leave (Switzer 1997; Haas 1998; reviewed in Switzer 1993). Such 'personal' information (Valone & Giraldeau 1993), however, is unavailable to nonbreeders and juveniles. Individuals may adopt three other types of breeding habitat selection strategies, depending on the information used: (1) strategies involving no information gathering, for example settle at random (i.e. with no direct respect to patch quality factors, Dale & Slagsvold 1990) or return to the natal patch (natal philopatry, Pärt 1991); (2) strategies using information on environmental factors affecting breeding success (e.g. presence of parasites or predators, Marzluff 1988; Boulinier et al. 2001; food availability, Brown & Brown 1996; vegetation type, Clark & Shutler 1999); (3) strategies using information on conspecifics, such as their presence ('conspecific attraction', Kiester 1979; Stamps 1988; Reed & Dobson 1993; Muller et al.

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1997), or their local reproductive success, assessed, for example, through the local density of juveniles produced (Desrochers & Magrath 1996; Danchin et al. 1998, 2001; Reed et al. 1999). However, despite this abundant empirical literature, little is known about the conditions that may favour the use of each type of information for breeding habitat selection in an evolutionary context.

Recently, the use of local (or patch) reproductive success of conspecifics, termed 'public information' (sensu Valone & Giraldeau 1993), has received increasing attention in empirical studies (Doligez et al. 2002 and references therein). It is thought to be a powerful cue for breeding habitat selection because it integrates the effects of all environmental factors on breeding success. Using patch reproductive success for breeding habitat selection may thus prove a more parsimonious strategy than assessing independently every abiotic and biotic factor potentially affecting breeding patch quality (Boulinier & Danchin 1997; Danchin & Wagner 1997; Danchin et al. 2001). The outcome of several local breeding attempts should also provide reliable information about local habitat quality, especially to failed breeders (Switzer 1997; Danchin et al. 1998) and individuals that cannot rely on their own reproductive success such as juveniles and nonbreeders (Boulinier & Danchin 1997). However, in many species information on patch reproductive success will be available only at the end of the breeding season, and thus can be used for breeding habitat selection only in the following year (Boulinier et al. 1996; Danchin et al. 1998). Therefore, breeding habitat selection strategies based on patch reproductive success the year before should be associated with a cost caused by this time delay. How and when the use of public information can be an evolutionarily stable strategy is thus a major issue which a modelling approach can help to tackle.

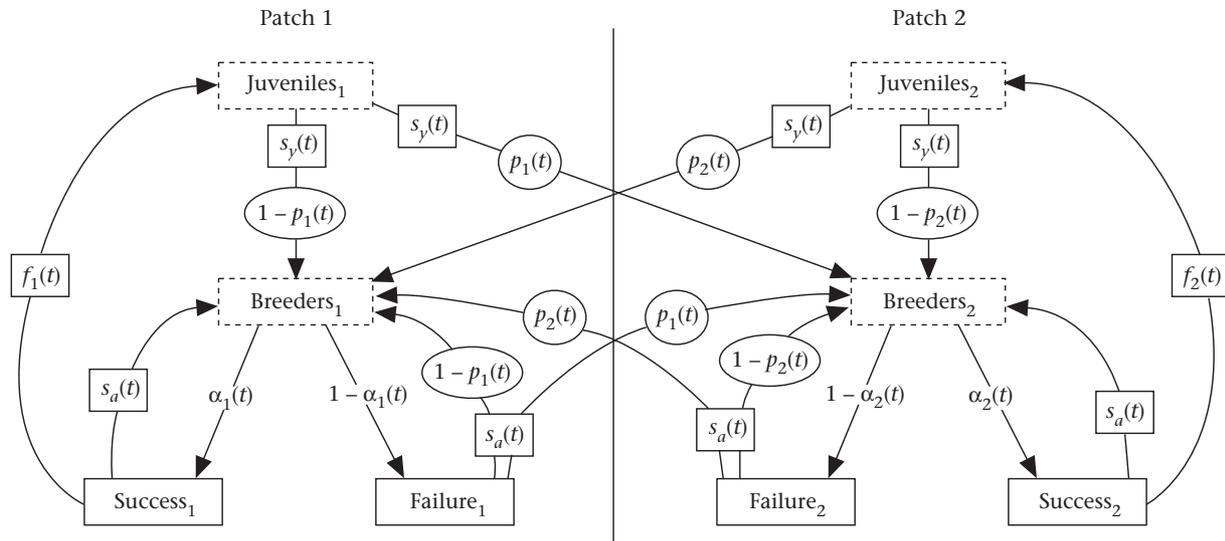
Using a theoretical approach, Boulinier & Danchin (1997) stressed the influence of the temporal predictability of environmental variations on the performance of strategies using public information. However, no interactions between individuals were considered in their simple optimality model, although both frequency- and density-dependent processes should affect the success of breeding habitat selection strategies, especially those using information conveyed by conspecifics. For instance, the success of individuals cueing on the mere presence of conspecifics should depend on the ability of already present individuals to settle on good-quality patches (Beauchamp et al. 1997), and thus on the frequency of strategies using other cues of patch quality in the population (Maynard Smith 1982; Heino et al. 1998). Furthermore, the fitness associated with a breeding habitat selection strategy should depend on the distribution of individuals across breeding patches through density-dependent processes. This distribution is in turn likely to depend on the breeding habitat selection strategies adopted by individuals. It is thus difficult to predict how such feedback effects will influence the evolutionary success of using public information compared with other strategies of breeding habitat selection.

We used a game-theoretical approach (Maynard Smith 1982; Dugatkin & Reeve 1998) to investigate how

environmental predictability, density dependence and frequency dependence can affect the evolutionary competitive outcome between a strategy of breeding habitat selection based on public information and strategies based on other information. Because personal breeding success should be an easily accessible (i.e. low cost) and highly reliable source of information integrating the effects of phenotype  $\times$  environment interactions, we assumed that breeders first rely on their own personal information. Successful reproduction reveals the ability of individuals to cope with the local environment, thus successful individuals should stay in their current breeding patch. Only failed breeders and individuals with no personal information (nonbreeders, juveniles) may use external cues for selecting a breeding patch (Danchin et al. 1998). The optimality of such a strategy is suggested by the high breeding patch fidelity of successful breeders observed in most species (see review in Switzer 1993 for birds). For failed breeders and juveniles, we investigated the evolutionary performance of a strategy of breeding habitat selection based on public information compared with strategies based either on no external information, or on other information gathered at the same time, that is, in the preceding year. Our aim was to assess how interactions between individuals affect the success of using public information for breeding habitat selection in environments of varying temporal predictability. Similarly, conspecific attraction has received theoretical support (Beauchamp et al. 1997), yet its success remains unclear when its tendency to aggregate individuals in space is taken into account. Finally, philopatry is classically viewed as a way for individuals to track local breeding habitat quality; however, its success still has to be assessed in temporally variable but predictable environments, especially when competing with strategies that update information on local quality. Our aim was to clarify these issues, and to assess whether environmental predictability and interactions between individuals are crucial factors that should be carefully examined when studying breeding habitat selection in the field.

## THE MODEL

The model depicts the female life cycle of a species with discrete breeding seasons. Individuals have the option of settling in either of two breeding patches of temporally variable quality as juveniles (natal dispersal) and as adults (breeding dispersal; Fig. 1). The number of breeding sites in each patch is unlimited, but only a proportion  $a_i(t)$  of adults breed successfully in patch  $i$  at time  $t$ . Successful breeders fledge  $f_i(t)$  juveniles, and are assumed to stay on their current patch to breed the following year. Thus, breeders preferentially use their own breeding success (or personal information, Valone & Giraldeau 1993) to assess patch quality (see above). Unsuccessful breeders in patch  $i$  at time  $t$  disperse to breed in the other patch at time  $t+1$  with probability  $p_i(t)$ , and thus stay with probability  $1-p_i(t)$ . Juveniles with no breeding experience are assumed to behave like unsuccessful breeders. Survival rates of adults and juveniles from  $t$  to  $t+1$  are noted  $s_a(t)$  and  $s_j(t)$ , respectively. The dispersal probability  $p_i(t)$



**Figure 1.** Diagram describing reproductive events and movements of individuals between two breeding patches.  $p_i(t)$ : probability that unsuccessful breeders and juveniles born in patch  $i$  at time  $t$  will disperse and breed on the other patch at time  $t+1$ .  $\alpha_i(t)$  (patch quality): probability that an adult will breed successfully in patch  $i$  at time  $t$  (i.e. fledge  $f_i(t)$  young).  $s_y(t)$  and  $s_a(t)$ : juvenile and adult survival rates between time  $t$  and time  $t+1$ . For further details, see Model section, [Tables 1](#) and [2](#).

defines the breeding habitat selection strategy, and depends on parameters determined for each strategy (see below). No explicit cost of dispersal or gathering of information on the environment per se is assumed. [Table 1](#) lists the parameters and variables used in the model.

We used the matrix approach ([Caswell 2000](#)) to model the dynamics of the metapopulation ([Appendix](#)). We first considered a short-lived species (low survival, high fecundity and no prebreeding period; [Table 2](#)). Because strategies of breeding habitat selection affect individual reproductive outcome, and because the sensitivity of growth rate to fecundity depends on the species' life cycle ([Stearns 1992](#)), we also tested the robustness of our results for a long-lived species (high survival, low fecundity and long prebreeding period; [Table 2](#)).

### Intraspecific Competition and Density Dependence

Demographic parameters are assumed to be affected by density as a result of intraspecific competition for resources. We consider that, during the breeding season, breeding success is negatively affected by the local density of adults in the patch. Thus, the mean number of offspring per successful breeder in patch  $i$  at time  $t$ ,  $f_i(t)$ , decreases with increasing breeding population size on patch  $i$  at time  $t$  ([Fig. 2](#)). Outside the breeding season, individuals compete with all conspecifics. Thus, survival rates  $s_a(t)$  and  $s_y(t)$  decrease with increasing total population size at time  $t$  (i.e. adults plus juveniles from both patches; [Fig. 2](#)). Therefore, fecundity and survival rates are both density dependent, but fecundity is patch specific whereas survival is not. Individuals adopting different strategies of breeding patch selection thus differ in fecundity, through patch choice, but not in survival.

### Temporal Autocorrelation of Patch Quality

The quality of patch  $i$  at time  $t$  is defined as the proportion of good (or successful) sites in this patch ([Boulinier & Danchin 1997](#)), that is, the probability of breeding successfully on patch  $i$  at time  $t$ ,  $\alpha_i(t)$ . Patch quality is 'intrinsic', that is, it does not depend on the number of breeders in the patch, and varies temporally. The extent to which the quality of patch  $i$  at time  $t+1$ ,  $\alpha_i(t+1)$ , may be predicted from its value at time  $t$ ,  $\alpha_i(t)$ , is measured by the temporal autocorrelation of patch quality ([Fig. 3](#)). The predictability of patch quality is formalized in the following way:  $\alpha_i(t+1) = AC \times \alpha_i(t) + E$ , where  $AC$  measures temporal autocorrelation of patch quality, and  $E$  represents random environmental variation in patch quality (see [Fig. 3](#) for details). We varied predictability from completely unpredictable (autocorrelation coefficient  $AC=0$ ) to highly predictable ( $AC=0.95$ ) patch quality, and also considered temporally constant environments (i.e. no change in patch quality).

### Strategies of Breeding Patch Selection

We consider five strategies that differ in information (if any) used by potential dispersers (juveniles and unsuccessful breeders) to decide where to settle ([Table 3](#)).

(1) Strategy 1, Random: individuals do not assess their environment, and choose their breeding patch randomly, that is, they have the same probability of settling on both patches.

(2) Strategy 2, Philopatry: individuals always return to their natal (and previous breeding) patch (strict natal philopatry).

(3) Strategy 3, presence of breeding conspecifics (Presence): individuals settle on each breeding patch in proportion to the previous year's relative density of breeders on each patch ('conspecific attraction').

**Table 1.** List of parameters and variables used in the model, and their definition

Parameter	Definition
<b>Life cycle variables</b>	
$f_i(t)$	Mean fecundity of successful breeders (i.e. number of juveniles produced) in patch $i$ at time $t$
$p_i(t)$	Probability that unsuccessful breeders and juveniles born on patch $i$ at time $t$ will disperse and breed on the other patch at time $t+1$
$s_a(t)$	Adult survival probability between time $t$ and $t+1$
$s_j(t)$	Juvenile survival probability between time $t$ and $t+1$
$n_i(t)$	Total number of breeders in patch $i$ at time $t$
$n(t)$	Total population size (adults plus juveniles from both patches) at the end of the breeding season at time $t$
<b>Environmental variables</b>	
$\alpha_i(t)$	Intrinsic patch quality, i.e. proportion of successful breeders in patch $i$ at time $t$
AC	Temporal autocorrelation coefficient
<b>Intermediate variables used for the analytical approach (AC=1)</b>	
$B_i(t)$	$s_a \alpha_i$ ; nondispersing fraction of the population on patch $i$ at time $t$ , at the resident equilibrium (i.e. surviving successful breeders)
$D_i(t)$	$(1-\alpha_i)s_a + \alpha_i f_i s_j$ ; potentially dispersing fraction of the population on patch $i$ at time $t$ , at the resident equilibrium (i.e. surviving unsuccessful breeders and juveniles)

$f_i(t) \times \alpha_i(t)$  is the mean number of fledglings produced per breeding individual in patch  $i$  at time  $t$ . In the analytical approach,  $\hat{\phantom{x}}$  means that the value depends only on patch densities of the resident at equilibrium, and  $'$  refers to values of parameters for the mutant strategy.

**Table 2.** Demographic parameters for the life cycles used in the model

Demographic parameter	Life cycle			
	Barn swallow		Kittiwake	
	Minimum	Maximum	Minimum	Maximum
Adult survival rate ( $s_a$ )	0.30	0.45	0.75	0.85
Juvenile survival rate ( $s_j$ )	0.10	0.30	0.60	0.70
Fecundity ( $f_i$ )	4	8	1	2
Age at first breeding	1		4	

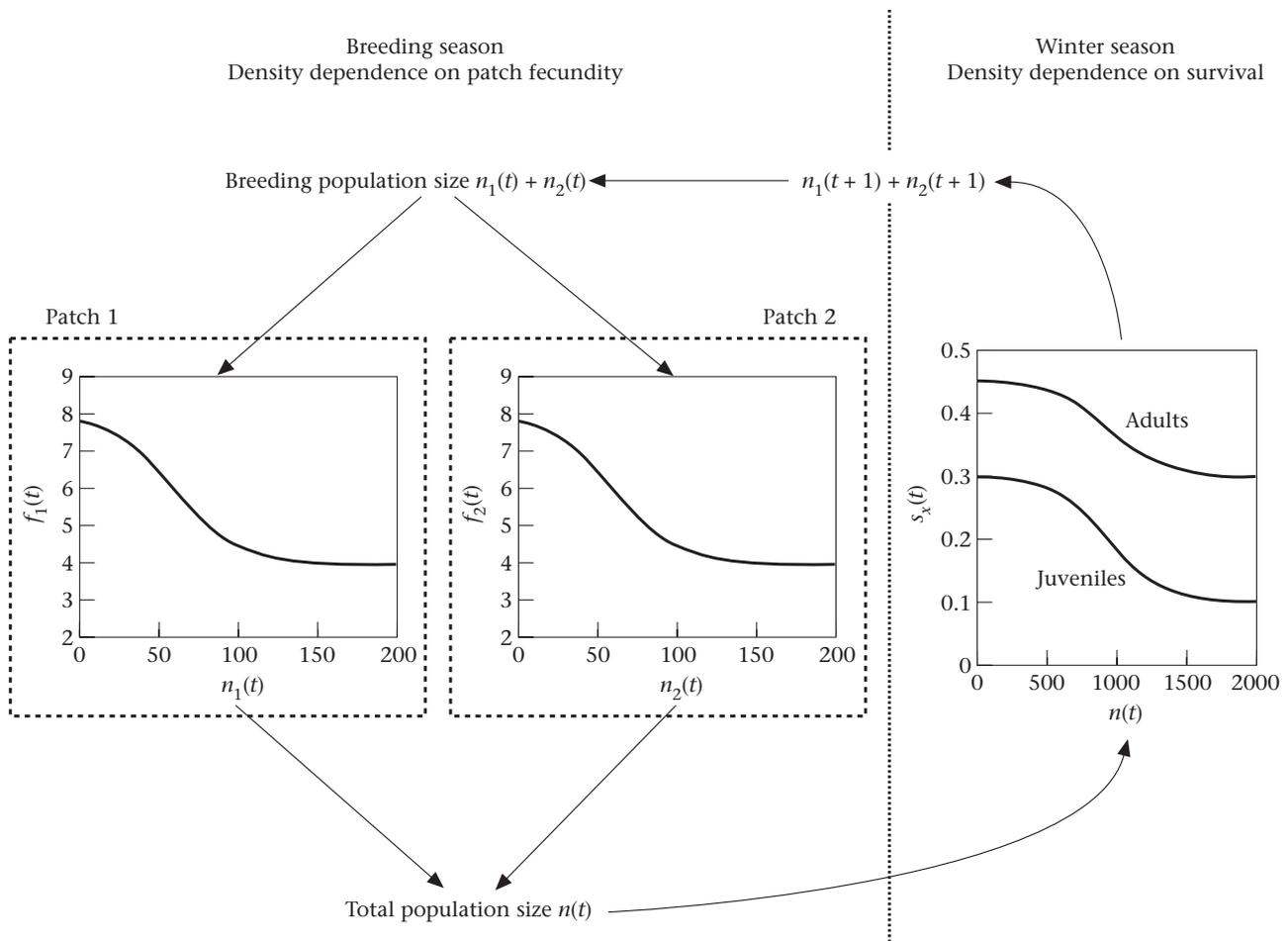
Values were chosen from Møller (1994) for the barn swallow, *Hirundo rustica* (short-lived life cycle), and from Danchin & Monnat (1992) for the black-legged kittiwake, *Rissa tridactyla*, in the North Atlantic (long-lived life cycle).

(4) Strategy 4, intrinsic patch quality (Quality): individuals settle on each breeding patch in proportion to the relative intrinsic quality of the two patches (here the relative probability of breeding successfully) in the previous year.

(5) Strategy 5, patch reproductive success (Success): individuals settle on each breeding patch in proportion to the relative patch reproductive success of conspecifics (i.e. mean number of offspring per breeding attempt) of the two patches in the previous year ('public information').

Our Presence, Quality and Success strategies all use information from the preceding year. We consider here that individuals do not update their assessment of patch quality by gathering information at the beginning of the breeding season (see Discussion). This allows us to compare the success of using different types of information while keeping the same time delay between information gathering and breeding patch choice. The Quality strategy (strategy 4) assumes that individuals have a complete knowledge of all potential environmental factors affect-

ing breeding success on a patch in year  $t$ , that is, they have access to intrinsic patch qualities at time  $t$ , to select their breeding patch at time  $t+1$ . In our model, patch quality is measured by the proportion of successful breeding attempts. Individuals would thus have access to the same information more parsimoniously by directly assessing this proportion. Quality may thus be seen either (1) as a strategy in which all factors influencing patch quality are assessed independently, or (2) as a strategy based on the proportion of successful breeding attempts, that is, another estimate of patch reproductive success. In both cases, what matters here is that the Success strategy differs from the Quality strategy because of density dependence on patch-specific fecundity (Table 3). While the Quality strategy is based only on intrinsic quality in the preceding year,  $\alpha_i(t)$ , the Success strategy is based on the actual mean fecundity achieved in the patch in that year (mean number of offspring per breeder),  $\alpha_i(t) \times f_i(t)$ , that is, it takes into account both the intrinsic quality  $\alpha_i(t)$  and the decrease in fecundity caused by density dependence.



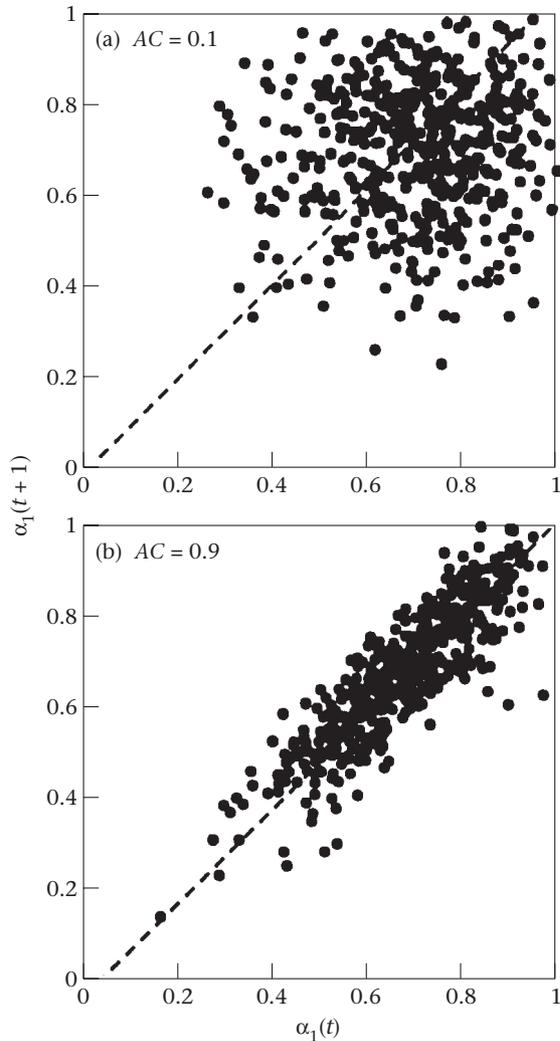
**Figure 2.** Density-dependent processes on life history traits. Density dependence is patch specific during the breeding season (patch fecundities) but not during the nonbreeding season (overall survival rates). The decrease in patch fecundity  $f_i(t)$  (mean number of fledglings per successful breeding individual in patch  $i$  at time  $t$ ) with increasing patch population size  $n_i(t)$  (number of breeders in patch  $i$  at time  $t$ ) is given by:  $f_i(t) = f_{\min} + (f_{\max} - f_{\min}) / \{1 + 0.05 \times e^{0.005 \times n_i(t)}\}$ , where  $f_{\min}$  and  $f_{\max}$  are, respectively, the minimal and maximal patch fecundities (Table 2). The decrease in survival outside the breeding season  $s_x(t)$  (survival rate of age class  $x$  between time  $t$  and  $t+1$ ) with increasing total population size  $n(t)$  (adults plus juveniles from both patches at time  $t$ ) is given by:  $s_x(t) = s_{x \min} + (s_{x \max} - s_{x \min}) / \{1 + 0.009 \times e^{0.005 \times n(t)}\}$ , where  $s_{x \min}$  and  $s_{x \max}$  are, respectively, the minimal and maximal survival rates for age class  $x$  (Table 2).

## EVOLUTIONARY STABILITY OF STRATEGIES

Optimal strategies of breeding habitat selection, in the absence of confrontation with other strategies, may not resist invasion by other strategies, that is, they may not be evolutionarily stable (Maynard Smith 1982; see e.g. Kokko 1999). Furthermore, in the presence of density dependence, no simple optimization criterion may exist, and evolutionary considerations should thus generally be based on an invasion criterion (Mylius & Diekmann 1995; Heino et al. 1998; Kisdi 1998). We tested both the ability of our strategies to resist invasion by rare mutant strategies when adopted by a resident population (evolutionarily stable strategies, Maynard Smith 1982), and their ability to invade a population when rare (Eshel 1983; Nowak 1990; Metz et al. 1996; Geritz et al. 1998). The five strategies were pitted against one another in pairwise contests, either as a mutant or as a resident. For practical reasons, we limited our approach to pairwise contests.

When an analytical approach was tractable, we used as the invasion criterion the growth rate of a rare mutant arising in a resident population at ecological equilibrium, noted  $\rho_{resident}(mutant)$ . The mutant strategy invades the resident one if this growth rate is strictly positive; otherwise, the resident strategy resists invasion (Metz et al. 1992, 1996; Geritz et al. 1998). The outcome of the confrontation between strategies A and B is predicted by calculating the two reciprocal growth rates  $\rho_B(A)$  and  $\rho_A(B)$  (each strategy either as mutant or resident): (1) A is selected if it invades B when mutant (i.e.  $\rho_B(A) > 0$ ) and resists invasion when resident (i.e.  $\rho_A(B) < 0$ ); (2) A and B coexist if both strategies are able to invade, but neither resists invasion (i.e.  $\rho_B(A) > 0$  and  $\rho_A(B) > 0$ ).

When an analytical approach was not tractable, we used numerical simulations to generate time series of patch quality with given autocorrelation levels (ULM software, Legendre & Clobert 1995). For each confrontation, simulations started with a resident strategy alone. The resident's matrix population was iterated 1000 time



**Figure 3.** Relation between temporal autocorrelation and predictability of patch quality. (a) When the autocorrelation coefficient is low, the value of patch quality at time  $t+1$  may not be predicted from its value at time  $t$ . (b) When this coefficient is high, the value of patch quality at time  $t$  is a good predictor of its value at time  $t+1$ . Temporal autocorrelation of patch quality is given by:

$$\begin{cases} \alpha_i(t+1) = \alpha_i(t) & \text{in temporally constant environments} \\ \alpha_i(t+1) = AC \times (\alpha_i(t) - \mu) + \beta(\mu, \sigma_c) & \text{in temporally variable environments} \end{cases}$$

where  $AC$  is the autocorrelation coefficient, and  $\beta$  is a beta function of mean  $\mu$  and variance  $\sigma_c$ ,  $\sigma_c$  being given by:  $\sigma_c = \sigma\sqrt{1-AC^2}$ . Only the level of temporal autocorrelation of patch quality varies (the variance of  $\alpha_i(t)$  is kept constant over time for all values of  $AC$  by the latter transformation). The initial quality of both patches was chosen randomly from the beta distribution. The  $\sigma_c$  value was chosen so that variation in patch quality would be as high as possible without causing  $\alpha_i(t)$  to leave the  $\{0;1\}$  interval too often (about 5% of cases). When that happened,  $\alpha_i(t)$  was randomly chosen between 0 and 1 again, and reinjected in the expression for calculation of  $\alpha_i(t+1)$ . Values of  $AC$  chosen: 0.0, 0.2, 0.4, 0.6, 0.8 and 0.95. Values of parameters:  $\mu=0.70$ ,  $\sigma=0.15$  (corresponding to the classical parameters of the beta function:  $a=5.83$ ,  $b=2.5$ ); these values were chosen to reflect plausible mean nest failure rate and variation between patches.

steps (one time step=1 year). Two mutant individuals with a different strategy of breeding patch selection were then introduced randomly into either of the two patches, in the successful breeder class, to give a short-term advantage to the mutant strategy to counteract immediate random extinctions. The two matrix populations were then iterated for the confrontation of both strategies until (1) the extinction of one strategy or stabilization of population sizes for each strategy (about 90% of confrontations), or (2) 50 000 time steps if extinction or stabilization had not occurred before then. As no demographic stochasticity was considered, we considered a strategy to be extinct when its total population size fell below one individual (total population sizes for both confronted strategies stabilized around 220 individuals for the short-lived life cycle, and 460 for the long-lived life cycle, including 220 breeders). The statistical behaviour of the mutant strategy in the stochastic environment was studied with Monte Carlo simulations (at least 100 simulations for each confrontation).

## RESULTS

In constant environments (fixed patch qualities), an analytical approach was tractable (Appendix). The Philopatry strategy resisted invasion (i.e. was an ESS), and invaded all other strategies although it was a 'weak invader' in some cases (Appendix). Therefore, Philopatry was always selected when the environment was heterogeneous in space but constant in time. Presence invaded Quality, Success and Random when patch qualities differed strongly, but otherwise coexisted with them (Fig. 4). Quality and Success performed better than Random; Quality invaded, and resisted invasion by, Success (Fig. 5 and Appendix).

When the environment varied temporally ( $AC < 1$ ), a formal analysis of the dynamics of the system was not possible, because the transition matrix from year  $t$  to  $t+1$  was both stochastic and density dependent (Caswell 2000). We therefore used simulations to study pairwise contests when  $AC < 1$  (simulations were also performed when  $AC = 1$  for comparison with analytical results; analytical and numerical results did not differ qualitatively). In temporally variable environments, many pairwise confrontations ended with stable polymorphisms, that is, both strategies coexisted at the end of simulations. Furthermore, the outcome of confrontations did not depend on the initial conditions (i.e. confrontations with A resident versus B mutant and B resident versus A mutant reached the same final state).

Figure 6 summarizes the general performance of all strategies according to environmental predictability for the short-lived species and Fig. 7 gives details of the outcome of pairwise confrontations. While dispersal was disadvantaged in temporally constant environments (Philopatry performed best when  $AC = 1$ , as stressed above), some level of dispersal was always favoured in temporally variable environments ( $AC < 1$ ; Fig. 6). The performance of Random progressively worsened with increasing temporal autocorrelation (Figs 6, 7a). For intermediate and high values of temporal autocorrelation,

**Table 3.** Dispersal probabilities of juveniles and unsuccessful breeders for the five breeding patch selection strategies

Breeding patch selection strategy	$p_i(t)$
Random	0.5
Philopatry	0
Presence of conspecifics (Presence)	$1 - n_i(t) / \{n_1(t) + n_2(t)\}$
Intrinsic patch quality (Quality)	$1 - \alpha_i(t) / \{\alpha_1(t) + \alpha_2(t)\}$
Patch reproductive success (Success)	$1 - f_i(t) \times \alpha_i(t) / \{f_1(t) \times \alpha_1(t) + f_2(t) \times \alpha_2(t)\}$

For the last three strategies, the linear response of dispersal probabilities to the cue used was chosen to reflect imperfect information acquisition and patch choice. When the value of the cue used is much higher in patch  $i$  than in the other patch, all dispersing individuals will settle and breed in patch  $i$ . But when the value of the cue becomes more similar between patches, there is growing uncertainty in the choice of patch. Successful breeders never disperse, accounting for the use of individual reproductive success (or 'personal information') in breeding patch selection (see text).

Quality and Success strategies were best (Figs 6, 7d, 7e). Their performances were similar when confronted with Random, Philopatry and Presence (Fig. 7a, b, c). However, when confronted with each other, Quality performed better than Success, especially in highly predictable environments (Fig. 7d, e). Finally, Presence and Philopatry were always low-performing strategies when  $AC < 1$  (Fig. 6), except Presence in unpredictable environments ( $AC = 0$ ; Fig. 7c). Presence was never alone at the end of confrontations even when numerically predominant (Fig. 7c). The general pattern of strategies' performance was very similar for the long-lived species (Supplementary Material), and thus seemed relatively unaffected by the life cycle.

### Evolutionary Mechanisms of Strategy Selection

Analytical results in temporally constant environments, for all strategies except Philopatry, allowed us to detail invasion mechanisms and identify the main forces explaining the performance of different strategies in environments of varying predictability level. In constant environments, a mutant strategy invaded the resident if and only if (Appendix):

$$(p'_1 - p_1)(\hat{D}_2(1 - \hat{B}_1) - \hat{D}_1(1 - \hat{B}_2)) > 0 \quad (1)$$

where  $\hat{B}_i = \hat{s}_a a_i$  and  $\hat{D}_i = (1 - \alpha_i) \hat{s}_a + \alpha_i \hat{f}_i \hat{s}_y$ ;  $\hat{\cdot}$  means that the value depends only on patch densities of the resident at equilibrium;  $p_1$  and  $p'_1$  are the probabilities of dispersing from patch 1 to patch 2 for a resident and a mutant, respectively ( $p_2$  and  $p'_2$ , dispersal probabilities from patch 2 to patch 1 for a resident and a mutant, respectively, are equal to  $1 - p_1$  and  $1 - p'_1$ ).

The first factor of the left-hand term of equation (1) measured the propensity for a mutant to disperse more from patch 1 (thus less from patch 2) than the resident; the second factor measured the level of aggregation on patch 1 (Appendix). Thus, if the quality of patch 1 is higher than the quality of patch 2 (i.e.  $a_1 > a_2$ ), the mutant strategy invaded in two cases: (1) if both factors were negative in the left-hand term, that is, if the mutant sent more individuals to the high-quality patch 1 than the resident when 'resident' individuals were about equally

spread across both patches, that is, it tracked patch quality more efficiently than the resident; or (2) if both factors were positive, that is, if the mutant sent more individuals to the low-quality patch 2 when 'resident' individuals were strongly aggregated on the high-quality patch 1, that is, it avoided paying the high cost in fecundity caused by spatial aggregation (Appendix, Fig. 4).

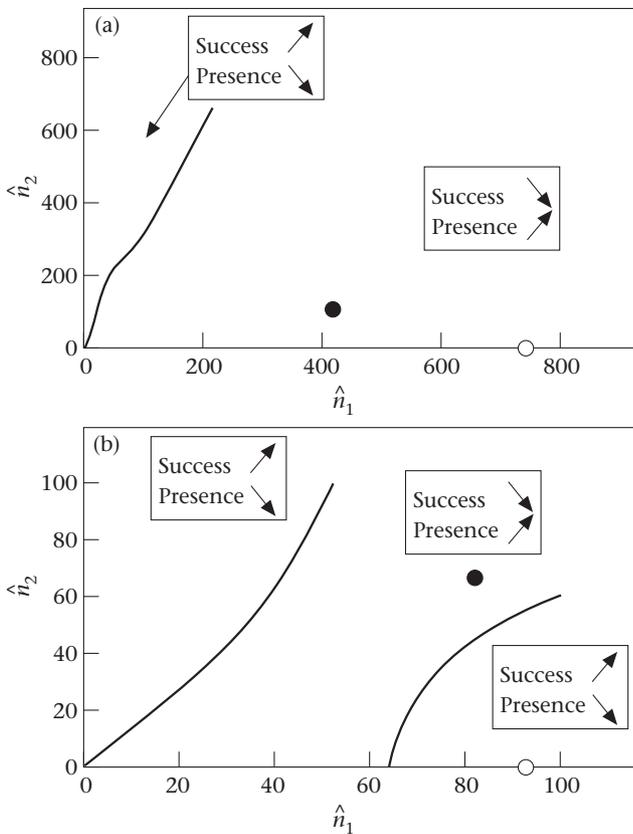
The evolutionary performance of the strategies was determined by the balance between these two mechanisms in constant environments, but also in most cases when temporal autocorrelation is less than 1. We illustrate these mechanisms below, along with two others that played a role in more specific cases.

### Tracking Patch Quality

The ability of a strategy to track variation in patch quality efficiently depended on environmental predictability. Individuals adopting the Quality and Success strategies were more efficient in settling in the better patch than those adopting Random, Philopatry or Presence when temporal autocorrelation was sufficiently high (Fig. 7d, e). When alone (no mutant introduced), Quality and Success led to more individuals on the better patch than the other strategies in highly predictable environments (Fig. 8a, b).

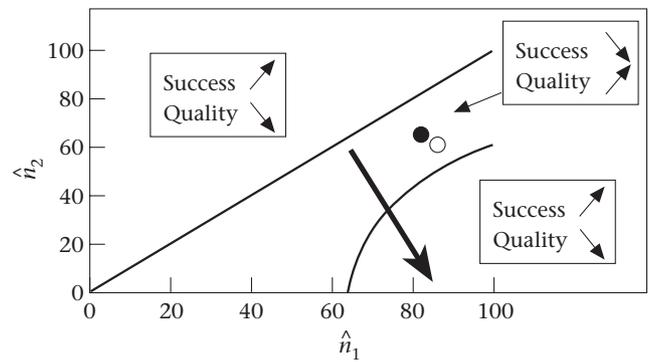
The Success strategy might have been expected to allow individuals to 'predict' the relative number of offspring expected on both patches the next year better than the Quality strategy in highly predictable environments, since Success combined information both on intrinsic quality and individuals' spatial aggregation. However, in highly predictable and constant environments, Quality performed better than Success (Figs 5, 7d), because the former led to higher aggregation on the better patch (Fig. 8). In such environments, Success thus tended to 'moderate' too much the assessment of relative patch qualities by the relative presence of breeders, through density dependence on fecundity, that is, Success was too 'reluctant' to send individuals to the better patch.

Although less efficient than Quality and Success, Presence also allowed individuals to track variation in patch quality in highly predictable environments,

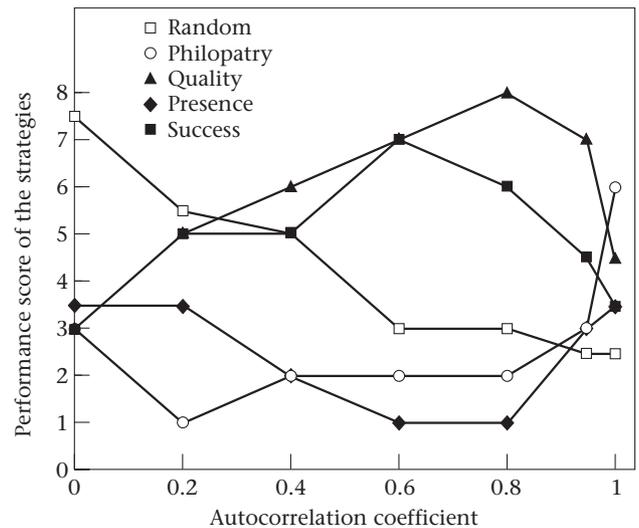


**Figure 4.** Confrontation of Success and Presence in a constant environment. The mutant fate in the confrontation is given as a function of patch densities at the resident equilibrium ( $\hat{n}_1, \hat{n}_2$ ). The two curves correspond to the right-hand term of equation (1) equal to zero. (Note that in a, the lower curve is too close to the X axis to be visible.) ↗: the mutant strategy invades; ↘: the mutant strategy goes extinct. If the resident equilibrium point ( $\hat{n}_1, \hat{n}_2$ ) falls between the two curves, Presence invades and Success does not; if ( $\hat{n}_1, \hat{n}_2$ ) falls outside these two curves, Success invades, and Presence does not. Circles show resident equilibriums (found numerically) of Success (●) and Presence (○) for (a)  $\alpha_1=0.6, \alpha_2=0.2$ , and (b)  $\alpha_1=0.4, \alpha_2=0.3$ . (a) Presence invades Success and resists invasion by Success; thus Presence is selected. (b) Presence invades Success, and Success invades Presence; thus the two strategies coexist. Presence is always more spatially aggregated on the better patch than Success which encourages individuals to leave the more highly occupied patch. When patch qualities differ strongly (a), Presence benefits from tracking patch quality more efficiently than Success despite the high cost of spatial aggregation, and Success cannot invade Presence. When patch qualities are more similar (b), Success benefits from paying a lower cost caused by density dependence (reduced fecundity) than Presence, because it aggregates individuals less; thus Success invades Presence despite tracking patch quality less efficiently, but is invaded by Presence when resident.

and thus performed better than Random when autocorrelation increased (Fig. 7c). The relative presence of breeders on the two patches the previous year reflected patch quality with a longer time delay (and less accurately) than the cues used by Quality and Success. As a result, temporal autocorrelation had to be high for Presence to perform better than Random (Fig. 7c).

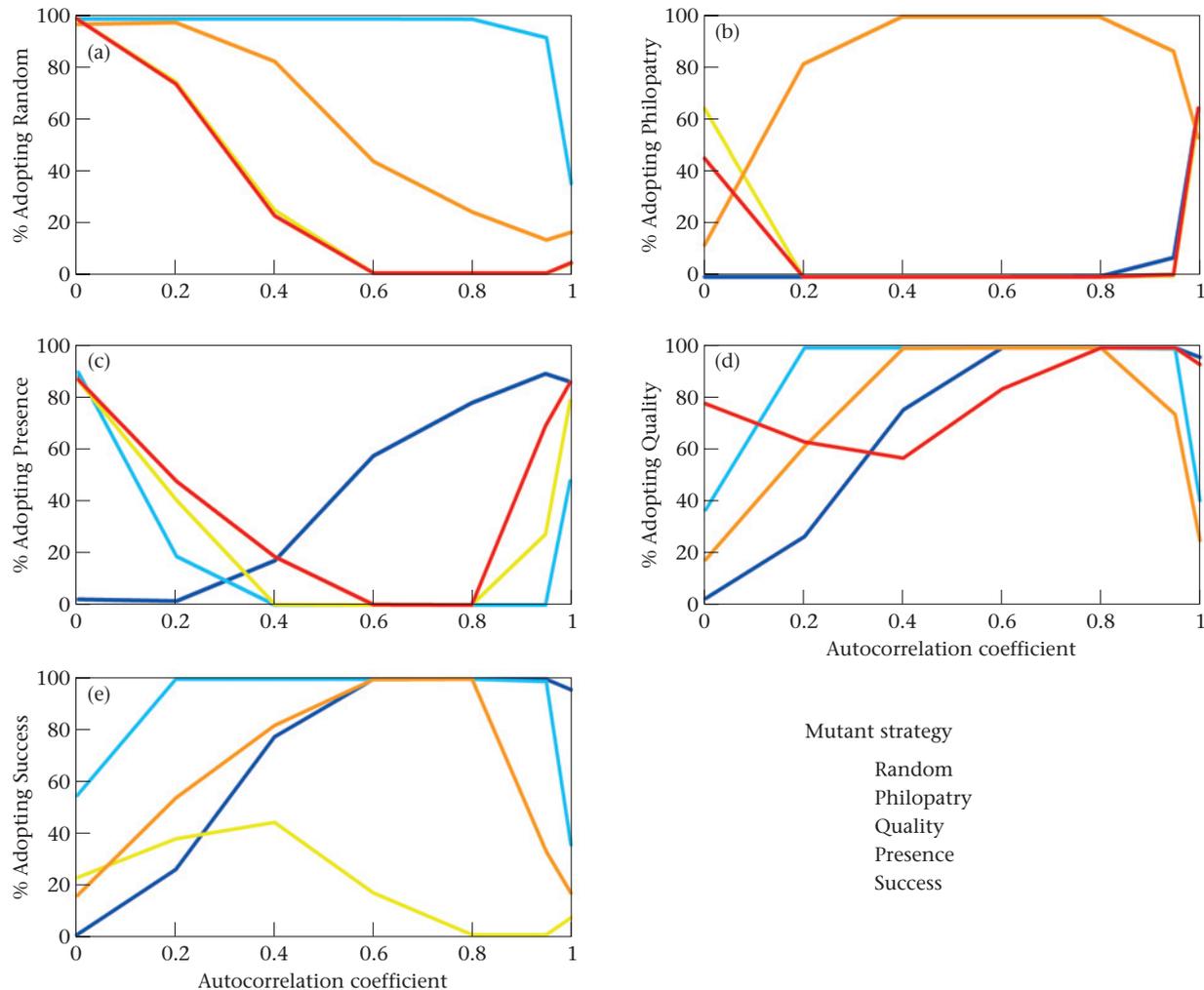


**Figure 5.** Confrontation of Success and Quality in a constant environment. See Fig. 4 for conventions. If ( $\hat{n}_1, \hat{n}_2$ ) falls between the two curves, Quality invades and Success does not. Otherwise, Success invades and Quality does not. Circles show resident equilibriums of Success (●) and Quality (○) for  $\alpha_1=0.4$  and  $\alpha_2=0.3$ . The arrow shows an increasing level of spatial aggregation. For all values of  $\alpha_1$  and  $\alpha_2$  in constant environments, numerical results show that Quality invades Success and resists invasion by Success. Thus Quality is the selected strategy in this confrontation, because it sends more individuals to the high-quality patch than Success (i.e. it tracks patch quality more efficiently).



**Figure 6.** General performance of the strategies of breeding patch selection when confronted with the others, according to the temporal autocorrelation coefficient, for the short-lived species. When the strategy was alone at the end of a confrontation (mutant total invasion or resident resistance to invasion), it was given a performance score of 1. When it coexisted with the other strategy, it was given a performance score of 0.5. When it went extinct, it was given a performance score of 0. The performance scores were then summed over all confrontations involving the strategy concerned. A given strategy was involved in eight confrontations (four as a resident, four as a mutant); thus the maximum possible performance was 8. □, ○: Unconditional strategies (sensu McPeck & Holt 1992); ▲, ◆, ■: conditional strategies (see text).

Presence also performed worse than Philopatry when the environment was to some extent predictable ( $AC>0$ ), suggesting that a strict return to the natal patch gave better rewards than using the relative presence of breeders



**Figure 7.** Detailed performance of the strategies of breeding patch selection in pairwise confrontations, for the short-lived species. The Y axis shows the percentage of the total population adopting the strategy concerned at the end of the confrontation with one of the four other strategies introduced as a mutant. Percentage of the population adopting (a) Random, (b) Philopatry, (c) Presence, (d) Quality, (e) Success, when confronted with the four other strategies as mutants.

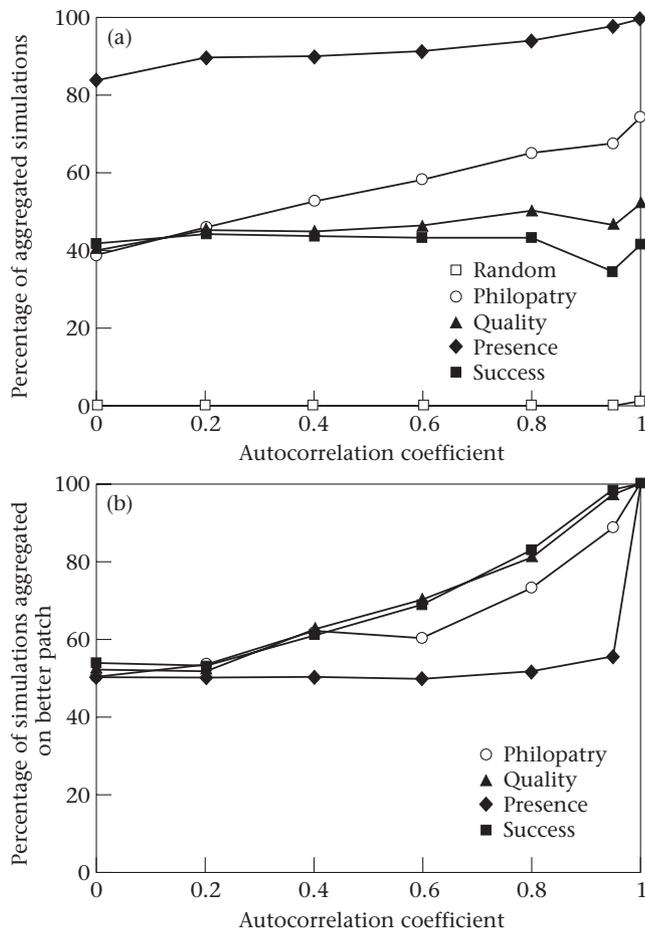
the previous year, because the information on the natal patch was less delayed.

Finally, in temporally constant environments, Philopatry allowed individuals to track spatial variations in patch quality better than the information conveyed by the local density of breeders or patch reproductive success the previous year as we modelled it here. In this case, Philopatry led to the Ideal Free Distribution (Fretwell & Lucas 1970; unpublished data), as could be expected since individuals distributed themselves proportionally to local resources (here measured by local breeding success). Thus when the environment was constant in time, Philopatry was favoured, that is dispersal was counterselected (Paradis 1998). The mere success of their parents reflected a high natal patch quality to individuals, which benefited from returning there even when no prior advantage to philopatric individuals was considered for the access to resources (Kokko & Lundberg 2001; Kokko & Ekman 2002). However, when the environment varied

temporally, returning to the natal patch did not guarantee that individuals would still find a good-quality breeding place.

### Avoiding the Cost of Spatial Aggregation

In weakly predictable environments, no strategy could efficiently track temporal variation in patch quality. Since strategies paid no explicit cost for information gathering, they might all have been expected to perform the same. However, Random was the best strategy in this case (Figs 6, 7a). Because there was no possible benefit of tracking patch quality in weakly predictable environments, strategies were inversely ranked according to their propensity to aggregate individuals in space, that is, to the density-dependent cost paid on fecundity. Random led to no spatial aggregation, thus paid no cost, while other strategies all generated a certain level of aggregation (Fig. 8a) and performed worse. Philopatry, Quality and Success led



**Figure 8.** Level of spatial aggregation generated by each strategy of breeding patch selection when alone (no mutant introduced), according to the autocorrelation coefficient, for the short-lived species. Spatial aggregation was assessed by comparing the observed distribution of individuals on both patches obtained with each strategy to a random distribution. The random distribution was modelled by a binomial distribution of probability 0.5 corresponding to the same probability of each adult breeding in each of the two patches. (a) Percentage of spatially aggregated distributions after 1000 time steps (i.e. percentage of simulations for which a random distribution could be rejected) on a total of 1000 simulations. (b) Percentage of these aggregated simulations for which aggregation occurred on the better patch (higher patch quality). The Random strategy was eliminated here as it did not generate significant spatial aggregation (see a).

to the same level of spatial aggregation when  $AC=0$ , and performed about the same.

Density dependence on fecundity also explains the poor performance of Philopatry when confronted with Random, Quality or Success (Fig. 7b). In the year following high quality in a patch, the high production of juveniles and the absence of a prebreeding period resulted in large numbers of individuals of the Philopatry strategy in this patch, and thus a high negative density-dependent effect on fecundity. Random, Quality and Success suffered less from density dependence, as they aggregated individuals less strongly (Fig. 8a), that is, they tended to spread individuals across both patches more equally than Philopatry.

### 'Parasitizing' Information from Other Strategies

As noted by Beauchamp et al. (1997) in the context of optimal foraging, the information conveyed by the relative presence of breeders on the two patches was not sufficient by itself, and needed to be 'complemented' with some other source of information. Individuals adopting the Presence strategy settled on patches depending on where other individuals had previously settled, that is, depending on the information gathered the year before and used by other individuals, whatever the patch qualities. Thus, they settled on the highest quality patch only if other individuals had settled there. This explains why Presence coexisted with the other strategy in all confrontations (Fig. 7b): Presence used (and was constrained by) the information conveyed by the other strategy (Supplementary Material). More generally, as shown in temporally constant environments, where the ability of a strategy to invade was determined entirely by the resident equilibrium (equation 1), all strategies when mutant (except Philopatry) indirectly 'used' information from the resident strategy.

Because of this parasitic nature, the Presence strategy can be related to the Scrounger strategy in producer-scrounger games developed in the context of social foraging (reviewed in Giraldeau & Caraco 2000). For both strategies, frequency dependence is acting to limit the proportion of 'parasitic' individuals: when this proportion increases (1) the reliability of information available to individuals of the Presence strategy decreases (Supplementary Material), and (2) the mean food intake of Scroungers decreases (Giraldeau & Caraco 2000). Conclusions generated by producer-scrounger game-theory models should thus also be useful in the context of information use for breeding habitat selection.

### Compensating for Spatial Aggregation

Another process explains why Presence performed better than Philopatry, Quality and Success in weakly predictable environments (Figs 6, 7c), even though it was then the most spatially aggregated strategy (Fig. 8a). In this case, successful individuals of the Presence strategy remaining on the 'emptier' patch experienced much lower density dependence on fecundity, thus achieved much higher reproductive outputs, than individuals of other strategies. This led to both a high mean reproductive success for Presence (10% higher than for the other strategies) and a large variance in reproductive success (2.5 times higher). These 'very' successful individuals compensated for the costs paid because of the high level of spatial aggregation. As soon as predictability increased, the value of the information used by Quality and Success increased (as shown by the increased aggregation of individuals on the better patch; Fig. 8b), and surpassed this effect. However, except for Presence in weakly predictable and temporally constant environments, the mean reproductive success for a strategy alone (no mutant) was not correlated with its performance in the confrontations.

## DISCUSSION

Our results show that environmental temporal predictability and density dependence can influence the long-term competitive outcome between different strategies of breeding habitat selection. In randomly varying ( $AC=0$ ) or constant ( $AC=1$ ) environments, strategies using no extra information are selected for. When habitat quality varies temporally, but in a sufficiently predictable way ( $0 < AC < 1$ ), using public information, that is, a measure of local reproductive success of conspecifics, to choose a breeding habitat the next year is a better strategy than choosing at random, being philopatric or using the mere presence of conspecifics. However, using public information is not always a better strategy than directly using intrinsic patch quality (without accounting for density-dependent effects). The strategies often coexist in the confrontations; in particular, the strategy based on conspecific presence always coexists with another strategy. The confrontation outcomes are determined by the interaction between the temporal dynamics of patch quality, and the way a strategy (1) allows individuals to track this variation efficiently, (2) leads to spatial aggregation of individuals, (3) parasitizes information from other strategies, and, less importantly, (4) compensates for spatial aggregation costs through variance in reproductive success.

### Temporal Predictability and Interactions

Previous theoretical studies stressed the key influence of temporal predictability of the environment on the evolutionary success of using personal (Switzer 1993) or public information (Boulinier & Danchin 1997) compared with other breeding habitat selection strategies. Our study confirms this result (1) when intraspecific competition and frequency-dependent processes are included, and (2) when a larger set of strategies is investigated. Predictability allows individuals to use cues gathered during the previous breeding season, and 'informed' strategies perform better than strategies using no information when the environment is predictable (but not constant). The importance of temporal predictability shown here questions the abundant theoretical literature addressing the influence of environmental variability on the evolution of dispersal and breeding habitat selection but considering only temporally constant or completely unpredictable environments for practical reasons (reviewed in Paradis 1998). This calls for more attention to the patterns of environmental temporal variability in further theoretical and empirical studies (see Stephens 1991 for the foraging habitat selection context).

Our study also emphasizes that interactions between individuals cannot be neglected (see also Forbes & Kaiser 1994; Kokko & Sutherland 2001 for the role of intraspecific competition in the context of access to breeding sites). Because the mean reproductive success obtained with a strategy outside confrontations is generally not a good predictor of its success in confrontations, density-dependent and frequency-dependent processes are crucial in determining the evolutionary performance of the strat-

egies, and shape the influence of temporal predictability. Density-dependent processes induce costs (here a reduced fecundity) for strategies that tend to aggregate individuals in space. Frequency-dependent processes are revealed in particular by the ability of the strategy based on conspecific presence to 'parasitize' the information used by other strategies (see below). The strength of density dependence, which is likely to depend on the nature of interference and competition processes between individuals, should strongly affect the evolutionary stability of the strategies of breeding habitat selection. In particular, one could expect the strategies based on public information to perform well under Allee effects (i.e. positive density dependence at low population sizes; Courchamp et al. 1999; Stamps 2001). In field studies, efforts should thus be made to disentangle the effects of density dependence from those of the dynamics of the distribution of individuals in relation to the heterogeneity of the environment.

### When to Use Public Information?

The strategy based on conspecific reproductive success performs better than the Random, Philopatry and Presence strategies when predictability is intermediate to high. Its low performance in constant or weakly predictable environments is due to its propensity to aggregate individuals in space, as already suggested by Boulinier & Danchin (1997) and Danchin et al. (1998). For intermediate predictability levels, using intrinsic patch quality directly is nevertheless a better strategy in some cases. But high costs of information gathering are expected for individuals to obtain full knowledge of intrinsic patch quality, and such a strategy should thus realistically be adopted only when individuals can assess local patch quality by using a few key factors. More parsimoniously, individuals could use here the local proportion of successful breeding attempts (see Methods); thus our Quality strategy could be seen as another form of use of public information. Consequently, our results suggest that public information cues are highly valuable in sufficiently predictable environments, but that different measures of public information may be used. At least some of the environmental components of habitat quality (microclimate, vegetation, predation pressure, ectoparasite infestation of nesting substrate, etc.) are likely to be temporally autocorrelated at various spatial scales (Boulinier & Lemel 1996). Thus, such environments should a priori be common in nature, even though few studies have actually documented the natural range of environmental predictability of patch quality in relation to habitat selection (Orians & Wittenberger 1991).

The timing of information availability is a key issue. Our modelling approach applies mostly to species unable to gather reliable information outside, or at the beginning of, the breeding season, for instance because of strong time constraints (Zicus & Hennes 1989), such as for migratory species (Slagsvold 1987; Reed et al. 1999). This situation should nevertheless be common, as cues available at the beginning of a breeding season are often much less correlated with the actual local reproductive success

in the season than the patch reproductive success of the preceding year (Boulinier et al. 1996; Brown & Brown 1996; Gowaty & Plisser 1997; Reed et al. 1999).

In natural populations, however, the quality and reliability of public information is likely to depend on (1) the interaction between intrapatch variability and information gathering processes, or prospecting (Reed et al. 1999), in particular the number of sites and patches sampled (Boulinier & Danchin 1997), (2) the similarity of individual responses to local conditions (i.e. genotype  $\times$  environment interactions), and (3) potential costs of information acquisition (Templeton & Giraldeau 1996; Giraldeau et al. 2002). Here, the Presence, Quality and Success strategies involved gathering external and potentially costly information. The presence of breeders may be assessed through the number of breeding pairs, or the number of empty breeding sites or families moving around at the end of the season. Directly assessing the intrinsic quality should involve gathering information on food availability, predation and parasitism risks, intra- and interspecific competition levels, etc., throughout the breeding season (see above). The mean number of offspring per breeding pair can be assessed via parental activity, or density of independent juveniles present at the end of the season (see empirical examples in the Introduction). Prospecting costs should be related to the breeding biology of the species: for example, reproductive success of conspecifics may be assessed more easily in colonial and open-nesting than in territorial and hole-nesting bird species, respectively (Danchin et al. 1998; but see Desrochers & Magrath 1996; Doligez et al. 2002). The existence and importance of costs of information acquisition, however, are difficult to assess, especially in highly mobile species such as birds and mammals, because (1) information can be acquired during other activities, thus implying no extra cost (Danchin et al. 2001), and (2) exploration may in itself be beneficial (Møller & Erritzoe 2001). When information gathering implies large costs, higher temporal autocorrelation will probably be required for a strategy based on local reproductive success to be selected. Therefore, species for which prospecting and information gathering costs are low may be expected to be more prone to using local reproductive success.

### Conspecific Attraction and Public Information

The overall poor performance of the strategy based on conspecific presence questions the abundant empirical and experimental literature on conspecific or social attraction (Kiestler 1979; Shields et al. 1988; Stamps 1988; Brown et al. 1990; Smith & Peacock 1990; Reed & Dobson 1993; Brown & Brown 1996; Lima & Zollner 1996; Muller et al. 1997; see also Forbes & Kaiser 1994). This apparent contradiction can nevertheless be explained. In many cases, the presence and success of conspecifics in breeding activities might have been confounded, and individuals might have been attracted by successful conspecifics (e.g. successfully courting bird models, Podolsky 1990; successfully incubating bird models, Veen 1977; successfully singing males, Alatalo et al. 1982; Eens 1994). More

specifically, individuals may be attracted not by conspecific presence per se, but by cues reflecting success at various stages of the breeding attempt and assessed through conspecific presence (Stamps 1988). Conspecific attraction has also been suggested as a way of aggregating so as to assess habitat quality more efficiently through the monitoring of conspecific reproductive success (Shields et al. 1988; Stamps 1988). Furthermore, conspecific attraction is a 'parasitic' strategy that uses the information of other strategies in the population through individuals' presence, as reflected by the systematic coexistence of this strategy with others. Thus, our results indicate that conspecific attraction should not necessarily be a rare strategy, and may be present in many populations even if it should not be used by all individuals in the population. If a fraction of individuals are attracted by conspecifics, while other individuals base their choice on other cues, this fraction is likely to be revealed by experiments on conspecific attraction. Such a demonstration of conspecific attraction may thus be an indication that other cues are also used in this population. Finally, studies on conspecific attraction have considered the presence or density of conspecifics in both the previous year (e.g. Gowaty & Plisser 1997) and the same year (e.g. Alatalo et al. 1982), that is, with and without a time delay. Here, we compared the evolutionary value of strategies using information gathered the previous year. Individuals might also update their patch quality assessment with information gathered at the beginning of the breeding season, such as conspecific presence or density, and thus adjust their breeding patch selection accordingly. Such strategies may be expected especially under strong intraspecific competition for breeding sites or mates.

### Expanding the Strategy Set

Although our breeding habitat selection strategies were chosen to be representative of the main strategies described in the literature, our strategy set is obviously not exhaustive. Including strategies based on other cues, however, should not change the main results. In particular, strategies using no information should dominate in weakly predictable or temporally constant environments; strategies based on integrative cues should be selected at intermediate levels of temporal predictability; and strategies relying on conspecific attraction should always coexist with another strategy by parasitizing its information.

The preferential use of personal success over other types of information could also be tested by allowing successful breeders to disperse as well. Successful breeders could disperse with the same probabilities as unsuccessful breeders (i.e. no use of personal information), or different information (personal versus external) may be allocated different weights. In our model the philopatry of successful breeders allows all strategies to track patch quality partly on the basis of the proportion of successful breeders (except Philopatry, for which there is no change). However, this advantage should be higher for Random and Presence than for Quality and Success.

Indeed, the Quality and Success strategies are already based on a cue that includes the proportion of successful breeders, while dispersers adopting the Random and Presence strategies use no information directly linked to breeding success. Assuming no use of personal information, for example that successful breeders behave as failed ones, should thus enhance the evolutionary success of Quality and Success; conversely, Presence may especially be disadvantaged, and cease to coexist with other strategies in some cases.

Similarly, we considered here for simplicity that unsuccessful breeders and juveniles were using the same strategy of breeding patch selection. However, unsuccessful breeders can partially rely on their own experience (here, a failure) to assess local quality, in contrast to juveniles. Distinguishing these two classes of dispersers would allow us to consider strategies such as 'win-stay, lose-switch' (Switzer 1993), where individuals always leave the patch after a breeding failure, which could apply only to breeders. Such distinctions, however, would increase the number of strategies and combinations of strategies to compare beyond a tractable limit without necessarily providing interesting insights. In particular, although we modelled a two-patch environment, we chose five strategies that can be generalized to a more realistic  $n$ -patch environment. In such environments, the decision of where to settle is decoupled from the decision to leave the current patch. A constant dispersal (i.e. emigration) rate or a dispersal rate conditional on personal success does not preclude individuals choosing between the remaining patches, either randomly or by using some information on local quality (Boulinier & Danchin 1997; Switzer 1997; Danchin et al. 1998).

### Population Level Consequences

The potentially high fitness of breeding habitat selection strategies based on public information has strong implications in evolutionary ecology. For instance, since habitat selection based on conspecific breeding performance directly affects the spatiotemporal dynamics of aggregates of breeding individuals in the environment, it may have led to the evolution of coloniality in species feeding on nondefensible food resources (Boulinier & Danchin 1997; Danchin et al. 1998). Furthermore, because it affects the dynamics of the use of habitat patches by individuals, it has implications for the conservation of small populations, notably in fragmented habitats. Habitat modifications arising from human activities may indeed decouple the cues used by individuals for breeding habitat selection from the true local quality of the environment, a process known as 'ecological trapping'. In this case, maladaptive breeding habitat choice leads to increased risks of population extinction (Delibes et al. 2001; Kokko & Sutherland 2001). Because public information cues correlate directly with habitat quality, their use in breeding habitat selection should not lead to ecological trapping. However, the occurrence of apparently suitable but empty breeding patches may result from the fact that individuals relying only on conspecific cues will never colonize new patches (Alatalo et al. 1982;

Shields et al. 1988; Stamps 1988; Smith & Peacock 1990; Reed & Dobson 1993; Forbes & Kaiser 1994). Strategies of breeding habitat selection based on public information may thus become evolutionary dead-ends because of local extinctions caused by demographic stochasticity or catastrophic events, especially in increasingly fragmented landscapes (Smith & Peacock 1990). Mixed strategies in which a small fraction of individuals ('pioneers', e.g. Toonen & Pawlik 1994) would select their habitat randomly or according to pure environmental cues are therefore likely to invade other strategies when local extinctions occur. Habitat selection strategies based on local conspecific success are clearly a key element to understanding the implications of individual behaviours on the functioning of natural populations (Sutherland 1996).

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### Appendix: Analyses in temporally constant environments (AC=1)

#### Ecological equilibrium of a strategy alone

If  $n_i(t)$  denotes the number of adults in patch  $i$  at time  $t$ , the transitions of patch population sizes from time  $t$  to time  $t+1$  are given by:

$$\mathbf{n}(t+1) = \mathbf{A}(\mathbf{n}(t)) \times \mathbf{n}(t) \quad (\text{A1})$$

where  $\mathbf{n}(t)$  is the vector  $(n_1(t), n_2(t))$  and  $\mathbf{A}(\mathbf{n}(t))$  is the following transition matrix:

$$A(\mathbf{n}(t)) = \begin{bmatrix} B_1 + D_1(1-p_1) & D_2 p_2 \\ D_1 p_1 & B_2 + D_2(1-p_2) \end{bmatrix} \quad (\text{A2})$$

with  $B_i = s_a a_i$  and  $D_i = (1 - a_i) s_a + a_i f_i s_y$ .

Note that  $\mathbf{A}(\mathbf{n}(t))$  is density dependent because  $s_a$ ,  $s_y$ ,  $f_1$  and  $f_2$  depend on  $n_1(t)$  and  $n_2(t)$ . Because of the complex-

ity of the density-dependent functions (Fig. 2), we cannot determine analytically the densities at equilibrium and their stability (except for the strategy Philopatry as described below). However, a stable equilibrium was reached in all numerical simulations we performed. Below, we use the properties of this equilibrium, on the assumption that the equilibrium of densities always exist.

#### Invasion of a mutant strategy

Let us consider now a mutant appearing in the resident population at equilibrium. Since the mutant is initially rare, we neglect it in the calculation of total patch densities and density-dependent traits; therefore, fecundities and survival rates depend on resident densities only. The superscript ' refers to the mutant, and  $\hat{\cdot}$  to values calculated at the resident equilibrium. The dynamics of the patch population sizes of the mutant are described by:

$$\mathbf{n}'(t+1) = \mathbf{A}'(\hat{\mathbf{n}}(t)) \times \mathbf{n}'(t) \quad (\text{A3})$$

where  $\mathbf{n}'(t)$  is the vector  $(n'_1, n'_2)$  and  $\mathbf{A}'(\hat{\mathbf{n}}(t))$  is the following transition matrix:

$$A'(\hat{\mathbf{n}}(t)) = \begin{bmatrix} \hat{B}_1 + \hat{D}_1(1-p'_1) & \hat{D}_2 p'_2 \\ \hat{D}_1 p'_1 & \hat{B}_2 + \hat{D}_2(1-p'_2) \end{bmatrix} \quad (\text{A4})$$

Note that dispersal probabilities of the Success, Quality and Presence strategies are also functions of resident densities at equilibrium, e.g. dispersal probabilities for Success are

$$p'_1 = 1 - \frac{\alpha_1 \hat{f}_1}{\alpha_1 \hat{f}_1 + \alpha_2 \hat{f}_2} = 1 - p'_2.$$

By definition, the initial growth rate of the mutant ( $\rho_{\text{resident}}(\text{mutant})$ ) is the logarithm of the dominant eigenvalue of matrix (A4):

$$\rho_{\text{resident}}(\text{mutant}) = \log(\lambda_{\text{resident}}(\text{mutant})),$$

with:

$$\lambda_{\text{resident}}(\text{mutant}) = \frac{1}{2} (\hat{B}_1 + \hat{D}_1(1-p'_1) + \hat{B}_2 + \hat{D}_2(1-p'_2) + \sqrt{(\hat{B}_1 + \hat{D}_1(1-p'_1) - \hat{B}_2 - \hat{D}_2(1-p'_2))^2 + 4p'_1 p'_2 \hat{D}_1 \hat{D}_2}) \quad (\text{A5})$$

The mutant invades if:

$$\rho_{\text{resident}}(\text{mutant}) > 0 \Leftrightarrow \lambda_{\text{resident}}(\text{mutant}) > 1 \quad (\text{A6})$$

*Philopatry strategy.* When the mutant strategy is Philopatry, equation (A5) simplifies to:

$$\lambda_{\text{resident}}(\text{Philopatry}) = \sup(\hat{B}_1 + \hat{D}_1, \hat{B}_2 + \hat{D}_2) \quad (\text{A7})$$

Let us show that  $\lambda_{\text{resident}}(\text{Philopatry}) > 1$ .

The total number of adults of the resident strategy on both patches at time  $t+1$ ,  $N(t+1)$ , is given by:

$$N(t+1) = (B_1 + D_1)n_1(t) + (B_2 + D_2)n_2(t) \quad (A8)$$

thus:

$$N(t+1) \leq \sup(B_1 + D_1, B_2 + D_2)N(t) \quad (A9)$$

At equilibrium, except in the trivial case where  $\alpha_1 = \alpha_2$ , and except for the Philopatry strategy,  $\hat{B}_1 + \hat{D}_1 \neq \hat{B}_2 + \hat{D}_2$ . Thus (A9) leads to:

$$\hat{N} < \sup(\hat{B}_1 + \hat{D}_1, \hat{B}_2 + \hat{D}_2)\hat{N} \quad (A10)$$

thus:  $\sup(\hat{B}_1 + \hat{D}_1, \hat{B}_2 + \hat{D}_2) > 1$ . As a consequence, Philopatry invades any other strategy.

When Philopatry is resident, its equilibrium is given by:

$$\begin{cases} \hat{B}_1 + \hat{D}_1 = 1 \\ \hat{B}_2 + \hat{D}_2 = 1 \end{cases} \quad (A11)$$

Using (A11) and  $p'_2 = 1 - p'_1$  for all strategies except Philopatry, equation (A5) reduces to:

$$\lambda_{\text{Philopatry}}(\text{mutant}) = 1$$

i.e. Philopatry is never invaded by a mutant strategy; thus it is an ESS.

*Random, Presence, Quality and Success strategies.* For these strategies,  $p_2 = 1 - p_1$  and  $p'_2 = 1 - p'_1$ . Combining (A5) and (A6), and using the fact that  $\lambda_{\text{resident}}(\text{mutant}) = 1$  when the mutant and resident strategies are the same, we obtain the following invasion conditions:

$$2 - (\hat{B}_1 + \hat{D}_1(1 - p'_1) + \hat{B}_2 + D_2 p'_1) < 0 \quad (A12)$$

or 
$$\begin{cases} 2 - (\hat{B}_1 + \hat{D}_1(1 - p'_1) + \hat{B}_2 + \hat{D}_2 p'_1) > 0 \\ (p'_1 - p_1)(\hat{D}_2 - \hat{D}_1 + \hat{D}_1 \hat{B}_2 - \hat{B}_1 \hat{D}_2) > 0 \end{cases} \quad (A13)$$

$$(p'_1 - p_1)(\hat{D}_2 - \hat{D}_1 + \hat{D}_1 \hat{B}_2 - \hat{B}_1 \hat{D}_2) > 0 \quad (A14)$$

(A12) is never true for these four strategies; thus the invasion condition reduces to equation (A14).

We can rewrite equation (A14) as:

$$(p'_1 - p_1)(\hat{s}_a(1 - \hat{s}_a)(\alpha_1 - \alpha_2) + \hat{s}_y[\alpha_2 \hat{f}_2(1 - \hat{s}_a \alpha_1) - \alpha_1 \hat{f}_1(1 - \hat{s}_a \alpha_2)]) > 0 \quad (A15)$$

Using this equation, we can show that a mutant strategy A verifying  $p'_1 < p_1$ , thus  $p'_2 < p_2$ , i.e. sending more individuals to patch 1 than the resident, invades only if

$$\frac{\hat{f}_1}{\hat{f}_2} \gg \frac{\alpha_2(1 - \hat{s}_a \alpha_1)}{\alpha_1(1 - \hat{s}_a \alpha_2)}$$

When patch 1 quality is superior to patch 2 quality, we can show that  $\hat{f}_1/\hat{f}_2 \leq 1$ . In that case, the above mutant A invades the resident only if  $\hat{f}_1/\hat{f}_2$  is close to 1, i.e. patch fecundities of the resident are close to each other, thus if the density of individuals of the resident strategy on the better patch is close to the density on the worse one. In other words, a strategy sending more individuals to the better patch than the resident, i.e. tracking patch quality better, invades the resident only if spatial aggregation of resident individuals on the better patch (here patch 1) is low.

On the other hand, we can show from (A14) that a mutant strategy B verifying  $p'_1 > p_1$ , i.e. sending more individuals to patch 2 than the resident, invades if

$$\frac{\hat{D}_2}{\hat{D}_1} > \frac{(1 - \hat{B}_2)}{(1 - \hat{B}_1)}$$

$D_i$  corresponds to (1) the probability that an adult in patch  $i$  at time  $t$  will be unsuccessful and survive, plus (2) the number of juveniles produced per successful adult in patch  $i$  at time  $t$ , that survive (see above);  $\hat{D}_i$  thus represents the potentially dispersing fraction of the population on patch  $i$  at the resident equilibrium.

$$\text{When } \alpha_1 > \alpha_2, \frac{(1 - \hat{B}_2)}{(1 - \hat{B}_1)} > 1.$$

Therefore, the mutant B for which  $p'_1 > p_1$  invades only when  $\hat{D}_2/\hat{D}_1 \gg 1$ , i.e. when the number of potential dispersers produced per adult in the low-quality patch 2,  $\hat{D}_2$ , is much higher than in the high-quality patch 1,  $\hat{D}_1$ , which implies that individuals of the resident strategy are strongly aggregated on the high-quality patch 1. In that case, the mutant invades because the aggregation of resident individuals generates high fecundity costs in the good patch because of density dependence. Individuals of the mutant strategy, which are more equally distributed across both patches than the resident, pay a lower cost in fecundity.