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The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species

THIERRY BOULINIER* and ETIENNE DANCHIN

Institut d'Ecologie, CNRS – URA 258, Université Pierre et Marie Curie, 7 quai Saint Bernard, 75252 Paris, France

Summary

Classical models of breeding habitat selection rarely deal with the question of information gathering for patch quality assessment. In this paper, we present two models comparing the fitness outcomes of behavioural strategies based on conspecific reproductive success as a cue to assess local environmental quality before selecting a new breeding habitat. The models deal with two phases of the life-cycle of a territorial migratory species: recruitment to a breeding population (model 1) and breeding site fidelity of subsequent breeding attempts (model 2). The first model shows that prospecting breeding patches before recruiting is the best strategy if the environment is predictable and contains a low proportion of good patches, even if it implies losing a breeding opportunity. The second model shows that dispersing after a breeding attempt according to the patch's breeding success rather than the individual's own success is the best strategy if the environment is patchy. These results underline the importance of studying the spatio-temporal variations of factors affecting reproductive success when considering the importance of habitat selection strategies based on conspecifics. Moreover, they allow the understanding of individual behaviour patterns observed in natural populations and their potential consequences at the metapopulation level.

Keywords: colonial breeding; conspecific attraction; dispersal; habitat selection; metapopulation; patchiness; predictability; prospecting; site fidelity

Introduction

Habitat selection is a prominent process in an individual's life and is likely to have constrained the evolution of several related life-history traits. Classical habitat selection models predict that individuals should be distributed in the environment so as to maximize fitness (Fretwell and Lucas, 1970). These models assume that individuals have free movement between patches and a perfect knowledge of the quality of the patches when they make a settling decision (Rosenzweig, 1991). More recently, the importance of patch quality assessment has been highlighted in an optimal foraging context by studies on the track of environmental fluctuations through sampling (Clark and Mangel, 1984; Abrahams, 1986; Stephens, 1987; Tamm, 1987; Bernstein *et al.*, 1988; Shettleworth *et al.*, 1988; Valone, 1989, 1993; Krebs and Inman, 1992; Pöysä, 1992; Valone and Giraldeau, 1993; Yoccoz *et al.*, 1993). Conversely, breeding patch selection has received little theoretical interest until recently (Switzer, 1993; Forbes and Kaiser, 1994), and models of dispersal rarely deal with the question of patch quality assessment (Waser, 1985; Holt, 1987; Johnson and Gaines, 1990; but see McPeek and Holt, 1992). Moreover, as breeding habitat selection usually concerns a longer time-scale than foraging patch selection (Orians and Wittenberger, 1991), it may

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*Address all correspondence to Thierry Boulinier, US Geological Survey, Biological Resources Division, Patuxent Wildlife Research Center, 11510 American Holly Drive, Laurel, MD 20708-4017, USA.

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be of direct relevance to the evolution of life-history traits (Stearns, 1992). Here we develop two simple models investigating the importance of a breeding habitat selection mechanism based on conspecific attraction (Stamps, 1987, 1988, 1991), corresponding to a simple type of social learning process (Boyd and Richerson, 1988).

In terms of breeding habitat selection, the quality of a patch is reflected by its potential for allowing the production of offspring (Cody, 1985). Since this potential is linked to many interacting factors, the best measure of patch suitability may be the actual current production of offspring by conspecifics rather than its physical and biological characteristics (Klopfer and Ganzhorn, 1985; Wiens, 1985). While breeding adults may use their own breeding experience to make breeding dispersal decisions (e.g. Brooke, 1978; Gavin and Bollinger, 1988; see Switzer, 1993, for a review), they may increase the amount of information available by looking at the reproductive success of conspecifics breeding on the same patch if there is low environment–phenotype interactions (E. Danchin, T. Boulinier and M. Massot, unpublished). Such information may be of particular value to first-time breeders who, by definition, have no previous breeding experience (Stamps, 1987, 1988; Shields *et al.*, 1988; Monnat *et al.*, 1990; Danchin *et al.*, 1991; Reed and Dobson, 1993).

To be able to make such decisions, however, individuals must gather information on the quality of potential patches. This also implies certain characteristics of the animals (sufficient cognitive and movement capacities, as well as survival) and of the environment (patchiness and predictability).

In this paper, we present two models comparing the fitness outcome of alternative behavioural strategies either using or not using conspecific breeding success as a cue to assess local environmental quality before selecting a breeding habitat. They concern two phases of the life-cycle of a territorial migratory species (Greenwood, 1980): recruitment to a breeding population and breeding site fidelity between subsequent breeding attempts. The models' predictions underline the importance of studying the use of conspecifics for reproductive decisions in relation to the spatio-temporal variation of factors affecting reproductive success.

The models

Model 1: The use of conspecifics for the first settling decision

Prospecting versus immediate breeding. This model concerns habitat selection at the first recruitment into the breeding population. The information available on breeding patch quality varies during the breeding season. Until the peak of fledging, the quantity and quality of information on the reproductive potential of a patch are likely to grow steadily. At fledging, the final output of a given patch can be assessed directly based on the proportion of successful nests, meaning that the prospectors should visit the different patches late in the breeding season to sample their environment before recruitment. Consequently, there is a trade-off between the potential fitness gain of reproduction early in life and the potential gain of sampling the habitat before starting to breed, and the strategy that leads to the highest fitness may depend on the type of variability of the environment.

Individuals can reproduce once a year and they have a probability, s, of surviving until the next year. If they breed successfully in a given year, they produce one offspring. We compare two strategies of habitat selection corresponding to different decision rules (see processes in Fig. 1A and 1B):

1. *Random settling strategy*: Individuals do not prospect before first breeding but settle randomly on a breeding patch and start breeding immediately. Individuals which breed successfully remain on the same patch the following year. Non-successful breeders disperse randomly the following year (see Fig. 1A).

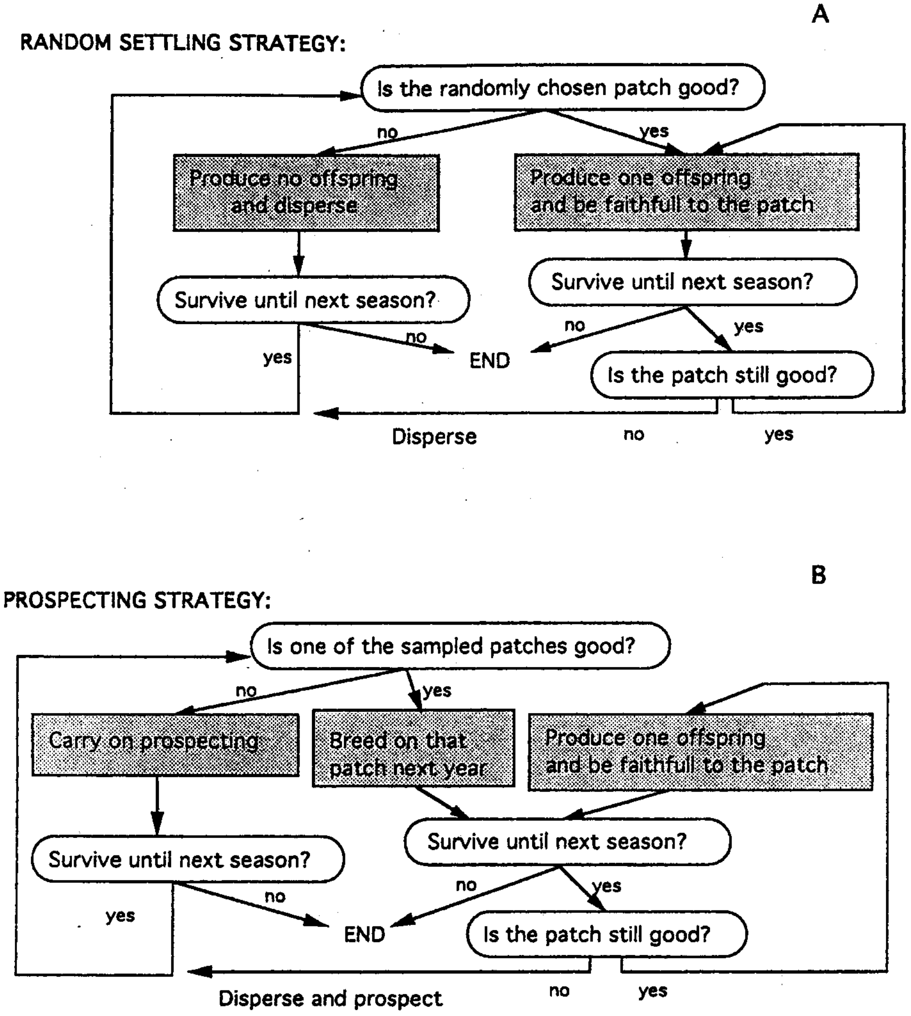

Figure 1. Flow charts for the random settling strategy (A) and the prospecting strategy (B) (model 1).

2. *Prospecting strategy*: Individuals prospect before first breeding: they spend time sampling the quality of different patches before choosing where to settle. They can prospect n breeding patches during any given year but do not breed in those years (incurring a cost). Individuals continue prospecting until they find a good patch (where they breed in the following year). If the patch becomes bad, they disperse and re-enter a prospecting phase the following year, according to the same rules (see Fig. 1B).

Characteristics of the environment. The environment is composed of an infinite number of good and bad breeding patches. The probability of breeding successfully is 1 on good patches and 0 on bad ones. The proportion of good patches, α, in the environment is fixed. There is no competition for site acquisition (i.e. patch size is infinite), nor an arbitrary cost to site acquisition or dispersal.

The model allows for variation in patch quality over time. The predictability of the environment is described by the temporal autocorrelation coefficient of patch quality, r, and is directly related to the probability that a patch of a given quality one year remains of the same quality in the following year (see Stephens, 1987; Switzer, 1993). The temporal autocorrelation coefficient, r, is computed so that the proportion of good patches, α, does not vary between years (see Appendix; Lebreton, 1981). Each type of patch has a given probability of changing states each year depending on r. If $r = 1$, patches never change in quality (i.e. constant environment), whereas if $r = 0$, the quality of a patch is not predictable from one year to the next.

Fitness measure. The mean lifetime reproductive success (LRS) associated with each of the two strategies is calculated as a function of the annual probability of survival, s, the number of patches sampled during a prospecting year, n, the proportion of good patches in the environment, α, and the temporal autocorrelation of patch quality, r. Estimates of mean LRS of both strategies were computed for each set of parameters through Monte Carlo simulations ($n = 2000$ runs).

Model 2: The use of conspecifics for breeding dispersal decisions

Fidelity rules based on own versus patch-breeding success. This model investigates the possible importance of using the breeding success of patch neighbours for breeding dispersal decisions. Among the factors that can affect the decision to change breeding patches between years, the quality of the breeding site is likely to be an important one (a site may be more or less exposed to predation, ectoparasites or bad weather conditions). This quality may vary at different spatial scales and, for instance, the environment may be made up of relatively homogeneous patches. Since an individual, even on a good patch, may fail in its breeding attempt due to a random event, it may be valuable for a breeder to make its dispersal decision according to some combination of its own breeding success and those of its neighbours. This model compares the reproductive outcome of a breeding dispersal strategy using patch information with the outcome of a strategy using the individual's breeding experience only.

The two strategies compared correspond to the following decision rules:

1. *Fidelity strategy based on own success.* Individuals that fail to breed disperse and settle randomly on a patch the following year. Those that breed successfully remain on the patch the following year.
2. *Fidelity strategy based on patch success.* Individuals do not rely on their own breeding success but make their dispersal decision in relation to yearly patch quality. If the patch is good, they remain on it the following year whatever their own breeding success. Otherwise, they disperse and settle at random on another patch the following year whatever their own breeding success.

Characteristics of the environment. The characteristics of the environment are the same as in the first model, except that the probabilities for an individual to breed successfully is β on a good patch and γ on a bad patch. For simplification, γ is fixed to $(1 - \beta)$ and $\beta > 0.5$.

Fitness measure. As in the first model, we computed the average LRS associated with the two strategies, as a function of the demographic (s) and environmental (α, β, r) parameters.

Results

Results of model 1: Prospecting versus immediate breeding

Effect of the proportion of good patches. In a temporally constant ($r = 1$) environment, the mean LRS of the prospectors is superior to that of non-prospectors when the proportion of good patches

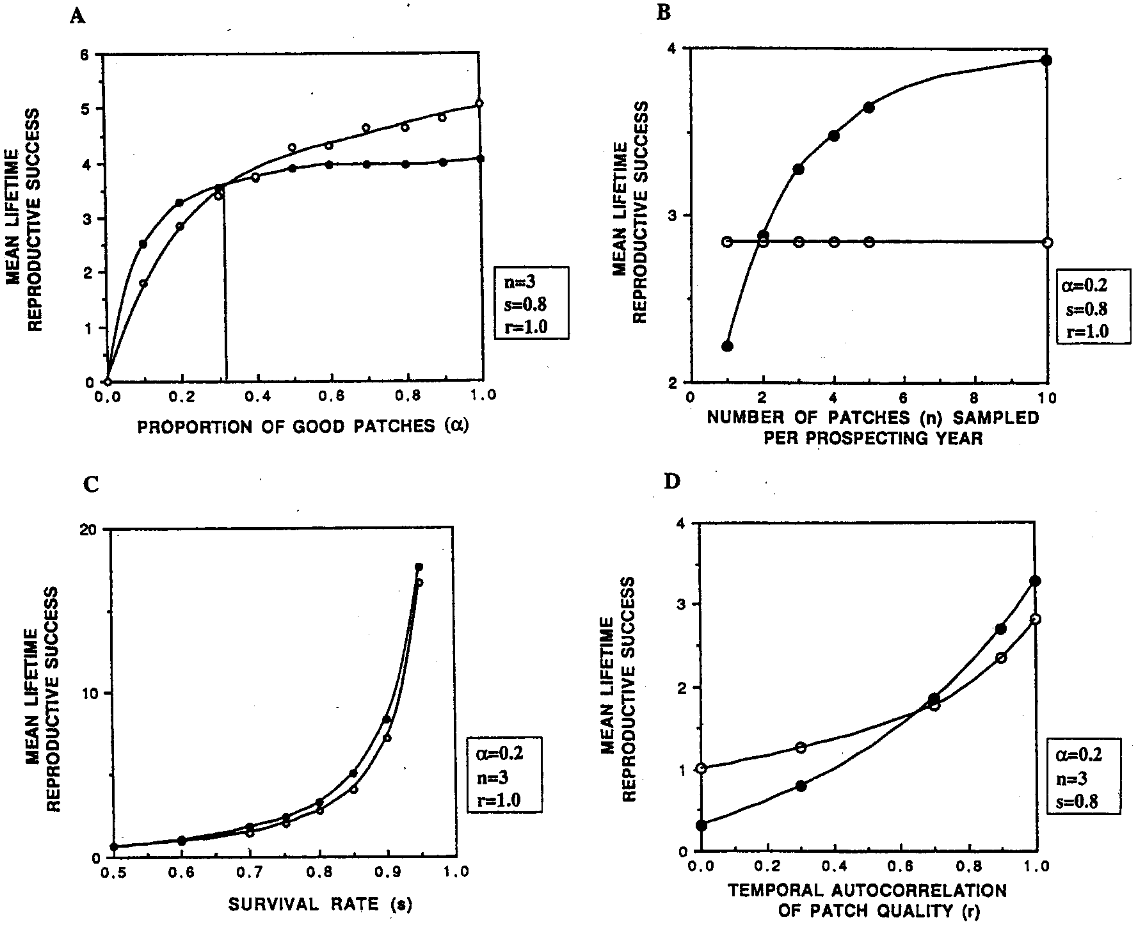

Figure 2. Effects of the proportion of good patches in the environment, α (A), the number of patches sampled during a prospecting year, *n* (B), the adult survival rate, *s* (C), and the temporal autocorrelation of the environment, *r* (D), on the mean LRS of the random settling (○) and the prospecting (●) strategies.

(α) is low (less than 30% with the set of parameters used in Fig. 2A). In such cases, the high cost associated with prospecting is compensated for by the benefit of finding a good site early in life. When the proportion of good patches is high, the prospecting strategy does not offer an advantage, because the probability of settling on a good patch by chance is high. The same pattern is found for other sets of parameters.

Effect of the number of patches prospected. The number of patches prospected (*n*) during a prospecting year greatly affects the fitness of the prospecting strategy (Fig. 2B). This strategy is, of course, defeated by the random settling strategy when only one patch is sampled per prospecting year, because in this case the cost of prospecting is not balanced by the benefit of sampling more patches (Fig. 2B). But, as soon as two patches are sampled, the prospecting strategy may have the higher fitness (Fig. 2B). The mean LRS of the prospecting strategy increases sharply with the increase in the number of patches sampled when this parameter is small (between 2 and 5) and levels off thereafter. Thus, in some environments, even the sampling of a relatively small number of patches per prospecting year can be a valuable strategy despite involving the lost opportunity to breed in these years.

Effect of the annual probability of survival. The annual survival rate, s, obviously affects the mean LRS of both strategies, but as soon as it becomes greater than 0.5, the prospecting strategy exceeds the random strategy for the basic set of parameters (Fig. 2C).

Effect of the temporal autocorrelation of patch quality. Introducing temporal variability in the quality of the patches reduces the mean LRS of both strategies (Fig. 2D). When there is no or little autocorrelation in patch quality (r equals or is close to 0), the random strategy beats the prospecting strategy: there is no interest in sampling patch quality, since it changes unpredictably from year to year. For the set of parameters used, the prospecting strategy wins when the level of temporal autocorrelation of patch quality is relatively high ($r > 0.65$; Fig. 2D). Other sets of parameters give the same results: the prospecting strategy has a higher fitness if the environment is sufficiently predictable and if only a small proportion of the sites are good.

Results of model 2: Fidelity rules based on own versus patch-breeding success

Effect of the proportion of good patches. Whatever the proportion of good patches (α), the fitness of individuals using their patch-breeding success for their breeding dispersal decisions is higher than that of individuals relying only on their own breeding success (Fig. 3A). The advantage is highest for intermediate values of α. There is little difference between the two strategies when the proportion of good patches is high, since the probability of being in a good patch is high for all individuals. Of course, when the proportion of good patches (α) is zero, the mean LRS of both strategies is the same.

Effect of the probability of breeding successfully on a good patch. The probability of breeding successfully on a good patch, β, affects the difference between the LRSs associated with the two strategies (Fig. 3B). Different values of β represent different levels of discrepancy between the information conveyed by personal and patch-breeding success. It is for intermediate values of β that the discrepancy is highest and the fidelity strategy based on patch-breeding success beats the one based on personal breeding success (Fig. 3B). For high values of β, failing in breeding is essentially equivalent to being on a bad patch and vice versa, thus both strategies are equivalent. For low values of β, there is only a slight difference between good and bad patches and relying on patch-breeding success does not improve greatly the mean LRS. Different values of the other parameters do not qualitatively change this result.

Effect of the annual probability of survival. The mean LRS of each strategy increases with increasing annual probability of survival, s, and is higher for the fidelity rule based on patch breeding success when $s > 0.5$ (Fig. 3C). The discrepancy between the two strategies increases with increasing s.

Effect of the temporal autocorrelation of patch quality. Introducing temporal variability in the quality of the patches reduces the mean LRS of both strategies. When there is no autocorrelation of patch quality (when $r = 0$), the two strategies result in the same mean LRS. But as soon as the temporal variation of the environment is slightly autocorrelated, the fitness of the fidelity rule based on patch-breeding success is larger than that of the rule based solely on the individuals' breeding success (Fig. 3D).

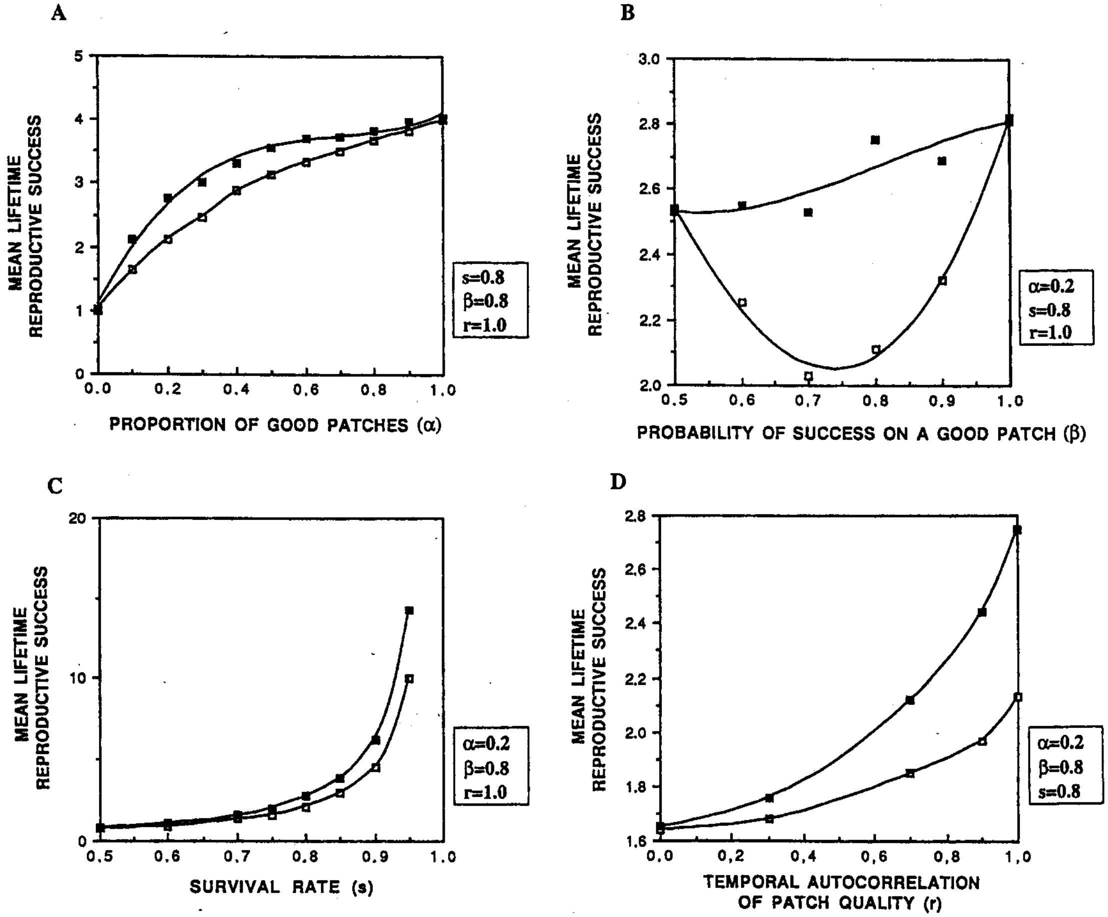

Figure 3. Effects of the proportion of good patches in the environment, α (A), the probability of success on a good patch, β (B), the adult survival rate, *s* (C), and the temporal autocorrelation of the environment, *r* (D), on the mean LRS of the site fidelity rules based on own (□) versus patch (■) breeding success.

Discussion

The two models developed here show that, under certain conditions, sampling the environment through conspecific reproductive success before taking settling decisions is the best strategy even if it entails a cost. In both models, the use of 'public information' (*sensu* Valone, 1989) is favoured if the environment is patchy and predictable. In the breeding habitat selection context presented here, the public information is the reproductive successes and failures of other individuals; in the foraging scenario, the public information is the foraging successes and failures of other individuals (Valone and Giraldeau, 1993; Templeton and Giraldeau, 1995).

The first model shows that a pre-breeding prospecting phase should be found in rather long-lived species (*s* and *n* large) breeding in environments where there is a small proportion of good patches (α low) and where patch quality is sufficiently predictable from one breeding season to the next (large *r*). We can also predict that such a habitat selection mechanism should lead to variations in the local prospecting rate in relation to patch quality. In turn, there should be a relation between local recruitment and previous-year patch-breeding success, even in species with delayed maturity.

Complex interactions among biodemographic traits and phylogenetic constraints are likely to have played major roles in shaping the pattern of delayed maturity observed in higher vertebrates (Stearns, 1992), and information gathering through prospecting may have been an important neglected factor in this perspective. In several bird species, immature individuals often spend years prospecting on conspecifics' breeding grounds (Porter and Coulson, 1987; Bradley and Wooller, 1991; Danchin *et al.*, 1991; Reed and Oring, 1992; Reed and Dobson, 1993; Cadiou *et al.*, 1994), despite such potential costs as competition for food in these areas (Furness and Birkhead, 1984). Prospecting usually occurs late in the breeding season (Danchin *et al.*, 1991; Boulinier *et al.*, 1996), a period when local breeding success provides good information on breeding patch quality (Zicus and Hennes, 1989). In the kittiwake, *Rissa tridactyla*, which breeds on cliff patches that appear of predictable quality, higher prospecting rates were recorded on the more productive patches (Cadiou, 1993), resulting in higher recruitment in those patches (E. Danchin, T. Boulinier and M. Massot, unpublished).

The potential importance of post-fledging exploration, notably in species breeding for the first time when 1 year old (Mead and Harrison, 1979; Baker, 1993), can also be inferred from this model. In particular, high temporal autocorrelation of the environment may explain the high levels of philopatry observed in several bird species (Greenwood, 1980; Harris, 1983; Furness and Monaghan, 1987; Shields *et al.*, 1988; Coulson and Nève de Mévergnies, 1992).

The second model shows that breeding site fidelity decisions based on local conspecific reproductive success should be found in species which breed in a predictable and patchy environment. From this we can predict that such fidelity rules should lead to a relation between the probability of dispersing and patch-breeding success, after controlling for individual breeding experience. After breeding on a bad patch, birds that disperse should tend to breed on a patch with a higher current breeding success than the one they left.

In most bird species, non-fidelity to the nest site occurs mainly after a breeding failure (Coulson, 1966; McNicholl, 1975; Brooke, 1978; Gavin and Bollinger, 1988; Podolsky and Kress, 1989; Gauthier, 1990; Beletsky and Orians, 1991; Weimerskirch, 1990; Sydeman and Emslie, 1992; Payne and Payne, 1993), but few studies have investigated the potential use of conspecific breeding success as a cue for dispersal decisions (Bollinger and Gavin, 1989; Bensch and Hasselquist, 1991; Orians and Wittenberger, 1991; Desrochers and Magrath, 1993; E. Danchin, T. Boulinier and M. Massot, unpublished). Using a dynamic modelling approach, Switzer (1993) showed that site fidelity based on personal breeding experience should be found in species living in heterogeneous and predictable habitats, and that the simple decision rule 'win-stay: lose-switch' is the optimal strategy in such environments. We extend this result by showing that using patch-breeding success, rather than personal breeding experience, should be favoured in such habitats. In the kittiwake, we found that, in some circumstances, neighbours' breeding success can indeed override personal breeding experience for site fidelity choices (E. Danchin, T. Boulinier and M. Massot, unpublished).

The factors acting on breeding success are more or less predictable and vary at different spatial and temporal scales corresponding to different levels of habitat selection (Morris, 1987). In most studies, the relative importance of each factor has been evaluated at a given time and in a given place, but few have focused on their scale of variation (Orians and Wittenberger, 1991). Moreover, the shape of the density dependence function that is likely to affect patch reproductive success does not necessarily monotically decrease with increasing local number of breeders (Brown *et al.*, 1990; Stamps, 1994). In the case of ectoparasitism by cliff ticks, for example, the effect on host breeding success is likely to vary according to the dynamics of infestation of the cliffs (Danchin and Monnat, 1992). Spatial and temporal autocorrelation analyses of parasite infestation would provide information on the scale of variation of this factor in relation to the host population behaviour observed (Loye and Carroll, 1991; Brown and Brown, 1992; E. Danchin, T. Boulinier and M. Massot, unpublished). Thus the type of spatio-temporal variations of the environment that are included in our models allows us to deal indirectly with the effect of such factors, and could be used as the basis for further investigations.

Realized habitat selection may not correspond to actual individual preferences (Wiens, 1985, p. 245), but rather may be affected by intraspecific competition for sites (Waser, 1985; Stamps and Krishman, 1990). For instance, the removal of experienced breeders from dense parts of a seabird colony was followed by the recruitment of younger individuals who were apparently prevented from breeding previously (Chabrzyk and Coulson, 1976; Potts *et al.*, 1980). The potential effect of intraspecific competition for sites was considered in a recent paper by Forbes and Kaiser (1994), who also applied the concept of public information to the selection of breeding habitat. In particular, Forbes and Kaiser suggest that local competition for sites and attraction to breeding conspecifics taken together may explain the presence of non-breeders in the colonies. Their models and ours are based on slightly different assumptions and provide two independent approaches that underline the potential importance of the use of public information for breeding habitat selection.

Mate choice follows the same kind of information-gathering process as breeding-patch selection (Dale *et al.*, 1990; Sullivan, 1994). These two aspects should be considered together, especially when dealing with polygynous species, where the question of restricted mate sampling appears to be of major importance (Slagsvold and Lifjeld, 1994).

Moreover, one must be cautious when applying the results of our models to a population of individuals (Mangel and Clark, 1988). The construction of a more realistic individual-based model would allow the investigation of the actual effects of local interactions and heterogeneities among conspecifics on the fitness of the settling strategies (Caswell and John, 1992), as well as their consequences at larger spatial scales (i.e. metapopulation dynamics; Pulliam and Danielson, 1991; Ray *et al.*, 1991; Smith and Peacock, 1992).

Such a model would help us to understand how such habitat selection behaviour could enhance the aggregation of breeding territories on previously successfully occupied patches and thus the global production of the population (Holt, 1987); in particular, it would be useful to investigate if, as previously suggested (Alexander, 1974; Shields *et al.*, 1988; E. Danchin, T. Boulinier and M. Massot, unpublished), such habitat-matching processes alone could lead to colonial breeding in species that reproduce in patchy and predictable environments and defend territories containing the nest only.

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Appendix

Patch qualities in year $t+1$ are defined, whatever the site, as an autocorrelated process, corresponding to the following conditional contingency table (Lebreton, 1981):

	Year (t)	
Year (t + 1)	**Good** (α)	**Bad** ($1-\alpha$)
Good	$(\alpha + r(1-\alpha))$	$(\alpha - r\alpha)$
Bad	$(1-\alpha-r(1-\alpha))$	$(1-\alpha+r\alpha)$
Total	1	1

With such a conditional table of probabilities, a marginal probability (α) of settling at random on a good patch in year t leads to the same probability in year $t+1$. r is the correlation coefficient between the two distributions.

Indeed, between year t and year $t+1$, the probability of a good site remaining good is $(\alpha + r(1-\alpha))$ the probability of a good site becoming bad is $(1-\alpha-r(1-\alpha))$. This gives for year $t+1$ a proportion of (α) good patches ($\alpha[\alpha + r[1-\alpha]] + [1-\alpha][\alpha - r\alpha] = \alpha$) and a proportion of $(1-\alpha)$ bad patches ($\alpha[1-\alpha-r[1-\alpha]] + [1-\alpha][1-\alpha+r\alpha] = [1-\alpha]$), respectively.

The use of this autocorrelated process allows the comparison of the two strategies in an environment with a fixed proportion (α) of good patches each year, but with the quality of these patches varying in a more or less predictable way from one year to the next, depending on the value of r.