Spatial and temporal variations of factors affecting breeding habitat quality in colonial birds: some consequences for dispersal and habitat selection

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Abstract
The aim of this paper is to investigate the potential importance of temporal variation of patch quality in habitat selection and metapopulation functioning of birds. The first part reviews our knowledge about the spatial and temporal variability of breeding patch quality and factors affecting reproductive success in colonial birds. This emphasises that several factors vary in time, depending on the scale considered. Furthermore some factors, such as predation or ectoparasitism, may follow particular patterns of temporal variation, resulting in a temporal autocorrelation of breeding habitat quality. Such autocorrelations may potentially affect dispersal behaviour. The second part presents a theoretical approach to the evolution of dispersal in a simple spatially and temporally varying environment incorporating some of the features of temporal variability described in part one. More specifically, our model describes some characteristics of the interaction between the Kittiwake and its nest ectoparasite, the tick Iodes uriae. We examine two levels of compensation for the cost of parasitism, and three levels of temporal variation. This shows that a dispersal strategy, which is favored in a particular case of temporal variation and level of compensation for the cost of parasitism, would be unfavored in another context. This result suggests that the temporal dynamics of the factors affecting breeding patch quality could have an effect on the dispersal behaviour observed. The third section proposes different approaches to further investigate the implications of environmental variability on dispersal and recruitment strategies, and metapopulation dynamics, using breeding success as an integrative measure of patch quality. We emphasize the need to incorporate complex behaviours in our model of the evolution of dispersal (such as the use of reproductive success of conspecifics by individuals to obtain information on patch quality). We indicate some possible approaches and the corresponding predictions and ways to test them empirically.

Keywords: Metapopulation, dispersal, habitat selection, evolutionary stable strategy, ectoparasitism, predation.
Résumé
Cet article analyse l'importance potentielle des variations temporelles de la qualité de l'habitat sur le choix d'un site de reproduction et le fonctionnement des métapopulations chez les oiseaux. Une première partie examine les connaissances disponibles concernant les facteurs qui affectent le succès reproducteur des oiseaux coloniaux. Cette section montre que plusieurs facteurs varient dans le temps, selon l'échelle considérée. De plus, dans certains cas, comme la prédation ou l'ectoparasitisme, ces variations suivent des schémas particuliers, entraînant une autocorrélation temporelle de la qualité de l'habitat de reproduction. De telles autocorrélations peuvent affecter le comportement de dispersion. Une seconde partie présente une approche théorique de l'évolution de la dispersion dans un environnement qui varie dans l'espace et dans le temps selon certaines des caractéristiques décrites dans la section précédente. Notre modèle est plus particulièrement basé sur l'interaction entre la Mouette tridactyle et la tique *Ixodes uriae*, qui parasite les nids de cet oiseau colonial. Nous examinons deux niveaux de compensation du coût du parasitisme et trois niveaux de variabilité temporelle. Les résultats montrent qu'une stratégie de dispersion qui est sélectionnée à un niveau donné de variabilité temporelle et de compensation du coût du parasitisme peut être défavorisée dans un autre contexte. Ceci suggère que la dynamique temporelle des facteurs affectant la qualité de l'habitat de reproduction est susceptible d'affecter le comportement de dispersion observé.
Une troisième partie propose différentes approches afin d'analyser plus finement les implications de la variabilité environnementale sur d'une part les stratégies de dispersion et de recrutement et d'autre part la dynamique des métapopulations, en utilisant le succès reproductif comme mesure intégrative de la qualité de l'habitat. Nous attirons notamment l'attention sur la nécessité d'incorporer dans notre modèle d'évolution de la dispersion des comportements complexes, comme l'utilisation par un oiseau du succès reproductif de ces conspécifiques afin d'obtenir des informations sur la qualité de l'habitat. Nous indiquons quelques approches possibles ainsi que les prédictions correspondantes et les moyens de les tester empiriquement.

INTRODUCTION

It is widely recognized that local breeding habitat (i.e., breeding patches) may differ in quality thereby leading to variation in expected probability of producing offspring (MAY & SOUTHWOOD, 1990). Such an idea has notably been emphasized by Pulliam's source-sink approach (PULLIAM, 1988), in which some breeding patches consistently produce an excess of individuals whereas others show a constant loss of individuals (due to differential local reproductive success and survival rates). In a similar way, the quality of each breeding patch may vary in time (PULLIAM, 1996). These spatial and temporal variations of breeding habitat quality are likely to affect animal dispersal behaviour (FRETWELL & LUCAS, 1970; JOHNSON & GAINES, 1990; LIDICKER & STENSETH, 1992). Numerous theoretical studies have explored how dispersal could evolve in a spatially and/or temporally varying environment (JOHNSON & GAINES, 1990; LEVIN & COHEN, 1991; MCPHEE & HOLT, 1992; WIENER & TULJAPURKAR, 1994; LEMEL et al., in press). However, these models do not incorporate the patterns of variability which have been empirically observed. In particular they ignore potential temporal autocorrelation of patch quality (LEGENDRE, 1993), which can affect their predictability. For instance, for a given environment and species, breeding patch quality may show a low temporal predictability which means that next years patch quality cannot be predicted accurately on the basis of the current year value of potential indicators (SWITZER, 1993). Conversely, the combination of factors affecting breeding habitat quality may render breeding patch quality predictable from one year to the next. These patterns of temporal variability may greatly affect the processes of dispersal and habitat selection (BURGER, 1982;
Temporal variations of habitat quality factors

BOULINIER, 1996). Of course, environmental predictability will depend on the
temporal and spatial scale considered, to which may correspond different levels of
habitat selection (MORRIS, 1987).

The aim of this paper is to investigate the potential importance of temporal
variation of patch quality in habitat selection and metapopulation functioning of
birds. In the first part, we review our knowledge about the spatial and temporal
variability of breeding patches for colonial birds. In the second part, we present
a theoretical approach of the evolution of dispersal in a simple spatially and
temporally varying environment incorporating some of the features of temporal
variability described in part one. Finally, we propose different approaches to further
investigate the potential implications of environmental variability on dispersal
and recruitment strategies, and metapopulation dynamics. Particular emphasis is
placed on the potential importance of conspecific-based breeding habitat selection
behaviours, the extent of which may have important effects on the distribution of
individuals among habitat patches, and is likely to depend on the spatio-temporal
dynamics of habitat quality (FORBES & KAISER, 1994; BOULINIER & DAUCHIN, in
press). Moreover, such habitat selection strategies may have strong implications for
the conservation of species living in fragmented habitats (SMITH & PEACOCK, 1990).

SPATIO-TEMPORAL DYNAMICS OF FACTORS AFFECTING
BREEDING PATCH QUALITY IN COLONIAL BIRDS

What is currently known of the spatio-temporal dynamics of habitat quality
in relation to dispersal and habitat selection? Can we determine some patterns
of variability that can be incorporated in theoretical models of the evolution of
dispersal? To examine these questions, we use colonial bird species as biological
models. We first present the reasons for this choice; then, we review our current
knowledge of spatio-temporal dynamics of the factors acting on breeding patch
quality.

Why colonial birds?

Some characteristics of colonial birds make them a particularly suitable group
for studying habitat selection and dispersal. First, they breed on discrete patches,
thus allowing easy monitoring of the dispersal and individual behaviour of marked
birds among and within patches (PÉVOT-JULLIARD et al., in press). Secondly, since
breeding sites are the only resource in the colony, habitat "quality" is directly linked
to the reproductive success of individuals (PERRINS & BIRKHEAD, 1983). And thirdly,
several studies have been carried out on the factors affecting reproductive success
of colonial birds, notably in the context of cost-benefit approaches of the adaptive
significance of colonial breeding (PERRINS & BIRKHEAD, 1983; WITTEMERGER &
HUNT, 1985; SHIELDS et al., 1988; BROWN et al., 1990). The occurrence of high
densities of breeders on the breeding patches emphasizes the potential importance
of various density dependent effects. Moreover, it allows one to analyse the effect
of environmental factors on patch quality from the survey of a large sample of
breeding attempts for each patch every year.

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Spatio-temporal dynamics of factors such as predation, ectoparasitism and food availability

While many studies have estimated the relative importance of each factor affecting habitat quality at a given time, few have focused on their spatial and temporal scales of variation (ORIANS & WITTEMBERGER, 1991). In particular, there is little published data on long-term temporal variation of habitat quality in non-colonial species (see SWITZER, 1993, for a review). YASUKAWA and SEARCY (1986) and DESROCHERS and MAGRATH (1993) studied year to year variations of territory quality by providing autocorrelations of harem size and reproductive success respectively for a sample of territories in two passerine species. Concerning colonial species, predation, ectoparasitism and food availability have been identified as potentially affecting the breeding success of colonies. Several studies relate colony size to the level of these factors (e.g., FURNESS & BIRKHEAD, 1984; BROWN & BROWN, 1986; SHIELDS & CROOK, 1987; MÖLLER, 1987; PARRISH, 1995), but little information is provided on their temporal dynamics. Nevertheless, some inferences can be made on the temporal and spatial scales of variation of predation, ectoparasitism, abiotic factors and food availability (CAIRNS, 1992).

Predation

At the scale of the colony, temporal variations of predation may follow different patterns. In some cases, the level of predation is likely to be temporally relatively constant. This is the case when predation depends on the physical structure of the colony. For example, risk of predation by large gulls on Puffins (Fratercula arctica) may vary with topography within a colony (steep versus flat areas; NETTLESHIP, 1972) and thus may appear constant in time. In Common Guillemots (Uria aalge), the structure of the ledges can influence the shape of the breeding group which affects rates of predation by Great black-backed gulls (Larus marinus, BIRKHEAD, 1977). In other cases, predation rates may vary in time independent of habitat structure. Predation by specialized individuals that may remain in a particular area, like in the case of corvids on kitiwake eggs, could occur during several consecutive years on a given site, and then disappear (DANCHIN & MONNAT, 1992). This is especially true of long-lived predators defending feeding territories, as for instance in skuas (ANDERSSON, 1976; TRILLMICH, 1978; TRIVELPIECE et al., 1980; BOULINIER, 1989a) and large gulls (TAYLOR, 1982; SPEAR, 1993). In small cavity nesting birds, predation may affect breeding adults, and thus have strong effects on both adult survival and local reproductive success (HARPENSTIST & YENEBERG, 1995). Predation may also vary on a regional scale, depending on the presence of the predatory species (WIEKLUND & ANDERSSON, 1994). Interactions among predators need to be considered. For instance, the presence of peregrine falcons may have had an indirect positive effect on local seabird reproductive success due to their effects on the corvids that were preying on the seabirds on an Alaskan island (PAINE et al., 1990). In conclusion, predation can induce a temporal autocorrelation of breeding patch quality which is likely to depend on the scale considered. However, very little data is available on the spatio-temporal dynamics of this factor.

Ectoparasitism

The effect of ectoparasites on their host should vary in space and time according to the dynamics of infestation of nesting patches. Ticks and bugs, which
complete their life cycle in the nesting substratum and are less mobile than fleas and blowflies, infest bird colonies and are suspected to affect host demography (LOYE & CARROLL, 1991; BOULINIER & DANCHIN, 1996). Little information is available on the dynamics of such hematophageous ectoparasites. A transversal survey of Kittiwake colonies of different ages showed that their level of infestation by the tick Ixodes uriae increased with the time since installation (DANCHIN, 1992a). This suggests that the local effect of such a factor may vary with time in a predictable way. These ticks were found aggregated among nests but not among nestlings within nests (BOULINIER et al., 1996), which may partly be explained by the heterogeneous distribution of the ticks in the cliff substratum. Detailed investigations of the dynamics of cliff infestation by this tick in the French Cap Sizun Kittiwake colonies showed that cliff prevalence of infestation was positively autocorrelated between successive years, but negatively after a time lag of several years (BOULINIER et al., unpublished). Such a pattern may be directly linked to the behaviour of the host population: colony desertion (DUFFY, 1983; LOYE & CARROLL, 1991), natal dispersal (BROWN & BROWN, 1992) and breeding dispersal (BOULINIER et al., unpublished) are associated with high local levels of infestation by such ectoparasites.

Abiotic factors

In the case of abiotic factors such as exposure to bad weather or high tides, the quality of sites may be very consistent among years. For example, Manx shearwater (Puffinus puffinus) burrows vary with respect to their susceptibility to flooding during heavy rain (THOMPSON & FURNESS, 1991). This can be viewed as an intrinsic lack of quality of some nest sites which may affect breeding site selection in this species. Nevertheless, considering such abiotic factors, the quality of the habitat may vary considerably in time. Flooding of the habitat of gulls and skimmers by tides affects their site tenacity (BURGER & SHISLER, 1980; BURGER, 1982). Group adherence behaviour, defined as the tendency to change sites among years, but to nest among the same neighbours has been associated with the low stability of the habitat of some species (McNICHOLL, 1975). In such cases, the spatial and temporal pattern of variation of flooding is likely to have a direct effect on the dynamics of colony size and colony persistence (GONZALEZ-DAVILA et al., unpublished).

Food availability

Despite the fact that little is known of the spatio-temporal variation of food availability, for long range foraging species, it is likely to vary on a very large spatial scale compared to the localization of the breeding sub-colonies or colonies (SCHREIBER & SCHREIBER, 1984; CAIRNS, 1989; DUNNET et al., 1990). Year to year variations of food availability may be dramatic and cause important breeding failures in seabirds (e.g., as recently in the Shetlands Islands, Scotland: BOULINIER, 1989b; HARRIS & WANGER, 1990; DANCHIN, 1992b; HAMER et al., 1993; UTTLEY et al., 1994). In some places such failures have been consistent through time (ROBERTS & HATCH, 1993). Correlative studies have shown that very large seabird colonies were associated with evidence of lower reproductive performance compared to smaller ones (GASTON et al., 1983; FURNESS & BIRKHEAD, 1984; HUNT et al., 1986). This suggests a negative effect of density, possibly associated with competition for resources on the breeding grounds (but see AIMLEY et al., 1995). Little is known of
the effects of local variations of food availability on demography (Cairns, 1992). Food availability could affect large scale dispersal of breeding birds, of which little is known (Coulson & Neve, 1992), but is less likely to affect dispersal on a more local scale. In Hirundinidae and Ardeidae, the presence of food near colonies might affect habitat selection on a small scale (Brown & Rannala, 1995).

**Interactions among the factors**

Finally, interactions among these factors and other density dependent effects participate in shaping the spatio-temporal variability of breeding habitat quality (Perrins & Birkhead, 1983; Wittenberger & Hunt, 1985). The resulting dynamics are likely to be difficult to infer. Nevertheless at each spatial scale, some factors are likely to explain most of the variations in patch quality (fig. 1). Processes of habitat selection in colonial birds may thus take place at the scale of the region, the colony or the sub-colony patch, depending on the relative importance of these different factors and according to the resulting level of spatial heterogeneity and temporal variability of breeding habitat quality (fig. 1).

![Diagram showing relationships between factors]

**SPATIAL SCALES:**
- Breeding patch scale
- Colony scale
- Regional scale

**TEMPORAL SCALES:**
- Predictable
- Unknown

Fig. 1. - Temporal and spatial scales of variation of environmental factors affecting reproductive success in colonial birds. Predation and ectoparasitism are likely temporally autocorrelated at the colony and sub-colony patch scales, but little is known on the temporal autocorrelations of the other factors (see text).
Conclusion

Although the main factors of habitat quality in colonial birds are known, only few studies investigated their long-term temporal variation. However, factors such as predation or ectoparasitism may vary in a predictable way, at least at a short time scale. Such patterns of temporal autocorrelation of habitat quality are likely to affect dispersal behaviour and thus the evolution of dispersal.

SPATIAL AND TEMPORAL VARIATION OF PATCH QUALITY:
SOME CONSEQUENCES ON THE EVOLUTION OF DISPERSAL

How can temporal variation of patch quality affect the evolution of dispersal? We investigate this question by developing a simple theoretical approach. Our model describes a long-lived species, such as a colonial seabird, living in a two-patch environment. Patch quality is affected by a local environmental factor that may follow different patterns of spatial and temporal variation. The model could correspond to different situations where a more or less temporally autocorrelated factor affects breeding patch quality. The particular example that was chosen corresponds to the interaction between the Kittiwake and the tick *Ixodes uriae*. These ticks are hematophagous ectoparasites which spend almost all their lives in the nesting substratum, feeding on their host only once for each of the three developmental stages. They appear to affect the local reproductive success of their host (Danchin & Monnat, 1992). As mentioned above, cliff prevalence of infestation by *Ixodes uriae* was found to be positively correlated between successive years, but negatively autocorrelated after a time lag of several years (Boulinier et al., unpublished). We thus investigated how the temporal patterns of variation of such a local environmental factor might affect the evolution of dispersal. We use a simple model where we compare asymmetric dispersal strategies. Prevalence of infestation was set to follow different patterns of temporal variation, corresponding to different levels of temporal autocorrelation. We use a matrix model (Caswell, 1989) and numerical simulations to determine the evolutionarily stable dispersal strategies.

Model development

The model considers only females that can occupy either of the two patches (or colonies). Within each patch, the population is divided in four age-classes: juveniles (0 year), immatures (1 year), subadults (2 years) and adults (≥3 years). Ectoparasites affect juveniles with a prevalence (proportion of juveniles parasitized) of $p_1$ and $p_2$ in patch 1 and 2 respectively. Each of the age-classes is divided into a parasitized and an unparasitized subpopulation. The demographic parameters can vary between these two categories of individuals as a consequence of parasitism. We assume that (1) dispersal is natal, i.e., only the juvenile stage can disperse between sites (at a proportion of $m_{12}$ and $m_{21}$ for movement from patch 1 to 2 and from 2 to 1, respectively); (2) the parasites affect juveniles after the dispersal phase, implying that parasites may not migrate and (3) all individuals survive during dispersal. Further we assume that the quality of the environment depends only on parasitism and the effect of parasites is identical at the two sites. Consequently, the
two sites differ from each other only in the prevalence of parasitism, which can vary both spatially and/or temporally. The demographic parameters for each age-class do not vary spatially and temporally. The model is schematically presented in figure 2.

Fig. 2. – Life cycle of the individuals in the metapopulation. $m_{ij}$ is the proportion of juveniles moving from site $i$ to site $j$. For unparasitized (up) and parasitized (p) individuals, we denote juvenile survival as $S_{ij}$ and $S_{pij}$, adult survival as $S_{iaj}$ and $S_{pai}$, and adult fecundity as $f_p$ and $f_p'$; immature and sub-adult survival are identical for parasitized and unparasitized individuals and are denoted respectively as $S_p$ and $S_{pi}$ respectively. See text for details.

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It is generally recognized that density-dependent effects are important in the regulation of bird populations (Perrins & Birkhead, 1983). In particular, it has been shown that annual reproductive success (i.e., the number of fledglings) may be negatively affected by colony size (Brown et al., 1990). We assume that within a patch, reproductive success, which corresponds in our model to the product of fecundity and juvenile survival, is affected by local adult density. We use a Beverton-Holt function to model density-dependence. Within each site, reproductive success of unparasitized individual at time \( t \) is:

\[
F_u(t) = F/(1 + k(N_{au}(t) + N_{ap}(t)))
\]

Where \( F_u \) is the product of juvenile survival \( (s_{uj}) \) and fecundity \( (f_u) \) of unparasitized individuals, \( F \) is a maximum potential reproductive success and \( k \) measures the strength of competition. \( N_{au}(t) \) and \( N_{ap}(t) \) are the patch densities of respectively unparasitized and parasitized adults.

According to empirical observations and experimental evidence (Moss & Camin, 1970; Möller, 1987; Chaplin & Georges, 1991; Boulinier et al., unpublished), we assume that ectoparasitism decreases the reproductive success of parasitized individuals as:

\[
F_p(t) = (1 - C) F_u(t)
\]

where \( F_p \) is the product of juvenile survival \( (s_{pj}) \) and fecundity \( (f_p) \) of parasitized and \( C \) is the cost of parasitism \( (0 < C < 1) \).

The dynamics of the populations of the two patches is described by the matrix equation (Caswell, 1989):

\[
N(t+1) = A(t)N(t)
\]

where \( N(t) \) and \( N(t+1) \) are the column vectors given by the densities of each age class in the two sites respectively at time \( t \) and \( t+1 \). \( A(t) \) is a transition matrix assembling the demographic parameters (i.e., survivals, reproductive success and migration rates) and the prevalences of parasitism. The transition matrix varies in time through the prevalence of parasitism and density dependence.

Basic reproductive rates

The basic reproductive rate \( (R_0) \) is the mean number of female offspring reaching maturity, produced per adult female over her reproductive life-span, in the absence of competition. We use \( R_0 \) rather than the multiplication rate of the population as a measure of the maximal fitness of a female. The latter corresponds to the dominant eigenvalue of the transition matrix and it is much more difficult to calculate than \( R_0 \). The basic reproductive rate can be defined for both unparasitized \( (R_{0u}) \) and parasitized \( (R_{0p}) \) individuals within each patch \( k \). \( R_0 \) for unparasitized individuals is (see Caswell, 1989, for the detail of the calculation):

\[
R_{0u} = s_{ui} F/(1 - s_{ua})
\]
where $F$ is the maximum potential reproductive success.

$R_0$ for parasitized individuals is:

$$R_{0p} = (1 - C) s_{p1} F / (1 - s_{pu})$$

Differences in survival rates between parasitized and unparasitized individuals can compensate for the cost of parasitism. We examine the following two cases:

1. total compensation for the cost of parasitism through an increase in the parasitized adult survival. The reproductive success and the adult survival of parasitized and unparasitized individuals differ within a site but their fitnesses are equal ($R_{0p} = R_{0u}$);

2. no compensation for the cost of parasitism (i.e., maximum cost to parasitism). Parasitized individuals do not compensate for their reduced recruitment and they have the same survival as the unparasitized individuals.

Temporal variations of parasite prevalence

To examine how temporal variation in patch quality acts on the evolution of dispersal, we investigated two cases. First, the prevalence of infestation varied in space but not in time. The environment was thus totally predictable. Second, prevalences of infestation varied in space and time, with different levels of temporal variation. Within each patch, the value of prevalence a given year was generated from the value of prevalence the previous year. Specifically, the prevalence of each patch at time $t + 1$, $p_1(t + 1)$ and $p_2(t + 1)$, was randomly selected from a normal distribution, truncated between 0 and 1, with a standard error SE and a mean equal to the values of prevalence at time $t$, $p_1(t)$ and $p_2(t)$. This process provides series of values positively autocorrelated for short time lags, but negatively for longer ones (fig. 3). The level of autocorrelation between successive years depends on the value of the standard error (fig. 3). When the standard error is small, the values of parasite prevalence in a patch between two successive years (i.e., $p_1(t)$ and $p_1(t + 1)$) have a high probability of being very close and the temporal autocorrelation of patch prevalence increases. When the standard error is large, the values for a patch between two successive years have a small probability of being very close and the temporal autocorrelation of patch prevalence decreases. Thus, SE can be used as a measure of the predictability of the environment: the predictability of the prevalence of infestation decreases when SE increases. We simulate three levels of temporal autocorrelation with the values of 0.1, 0.5 and 1 for the standard error (fig. 3).

Optimization technique and numerical simulations

Any pair $(m_{12}, m_{21})$ constitutes a dispersal strategy. Each of these strategies is characterized by a transition matrix, $A(t)$, differing from the others only in the dispersal rates. We iterate equation (3) to determine which dispersal strategies are evolutionarily stable. These strategies can never be invaded by any alternative strategy (see PARKER & MAYNARD-SMITH, 1990). Analytical expressions for the ESSs are difficult to obtain due, in part, to the complexity of the population model. Rather we present both analytical expressions and numerical results of an algorithm.
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Fig. 3. - Temporal autocorrelogram of simulated time series of prevalence with different Standard Errors ( ■ for SE = 0.1, ● for SE = 0.5 and ▲ for SE = 1), illustrating the different patterns of temporal autocorrelation produced. Black symbols represent significant autocorrelation coefficients (Moran's I) at the 0.05 level. When SE was low (SE = 0.1), prevalence was positively autocorrelated for short time lags, but negatively for longer ones. When SE was large (SE = 1), there was almost no significant temporal autocorrelation.

to describe the ESS space. Numerical simulations were conducted using the software program ULM (LEGENDRE & CLOBERT, 1995). $m_{12}$ and $m_{21}$ were chosen equal to 0.0, 0.1, 0.2, ..., 0.9, 1.0. Consequently, the set of all possible dispersal strategies, is $W = \{(0, 0), (0, 0.1), (0, 0.2), ..., (1, 0.8), (1, 0.9), (1, 1)\}$. The details of the numerical algorithm are described elsewhere (LEMEL et al., in press).

Baseline parameter values

Colonial seabirds are generally long-lived species, with high survivals and low fecundities. We used the following demographic parameters of the kittiwake (DANCHIN & MONNAT, 1992): 0.7 for juvenile survival, 0.8 for immature survival, 0.85 for sub-adult and adult survival and 1 for adult fecundity. We employed the single value of 0.5 for the cost of parasitism, $C$ and we assumed no differences between parasitized and unparasitized individuals in competitive ability, $k$, assigning
it a value of 0.01. We explored the case in which the difference of quality between the two sites is high. When prevalences were constant in time, we used the values 0.1 and 0.9 for respectively $p_1$ and $p_2$. As a consequence, patch 2 is the most parasitized patch. When prevalences varied through time, we used these values for $p_1$ and $p_2$ at time $t = 0$ and the three values of the standard deviation.

**Results**

The selected dispersal strategies depended on a combination of two factors which are (1) the presence or absence of a compensation for the cost of parasitism and (2) the level of temporal variation of prevalences. We discuss each particular case in detail below.

**Total compensation for the cost of parasitism**

Here, the cost of parasitism is totally compensated through an increase in survival of parasitized adults. There is a short term cost in terms of reproductive success but, on the long term, parasitism has no effect on the fitness of individuals. We found that the ESSs depended on the temporal variation of prevalences. When prevalences were constant in time, many dispersal rates were simultaneously ESSs. When prevalences varied in time, only one dispersal strategy was an ESS. Its value did not depend on the level of temporal variation of prevalences.

- *Temporally constant prevalences of infestation*

Here the prevalences of infestation varied only spatially and the environment was thus totally autocorrelated. McPhee & Holt (1992), Doebeli (1995) and Lemel et al. (in press) used a two-patch model with no parasitism to study the evolution of dispersal in a spatially varying but temporally constant environment. They showed that evolutionarily stable dispersal strategies occur when the realized fitness at equilibrium, i.e. fitness in the presence of density dependence, is equal to unity within each habitat. To test whether this condition is satisfied by our model, we found analytically that when the realized reproductive rates at equilibrium of parasitized and unparasitized individuals are equal to unity in each site, the relation between $m_{21}$ and $m_{12}$ is:

$$\frac{m_{21}}{m_{12}} = \frac{(p_2 C + 1 - C)}{(p_1 C + 1 - C)}.$$

When equation (6) is verified, the sites exchange the same number of individuals and the ratio of the dispersal rates is the inverse of the ratio of the equilibrium densities of immatures in each patch.

Using equation (6), we replaced $p_1$, $p_2$ and $C$ with their values, respectively 0.1, 0.9 and 0.5. Our numerical simulations showed that any dispersal strategy verifying equation (6) was never invaded by a strategy not satisfying equation (6) and coexisted with any strategy conforming to condition (6). This result suggests that the set of ESSs is a straight line in $(m_{12}, m_{21})$ space (fig. 4). As would be expected, the proportion of individuals which disperse is higher from the more parasitized patch (i.e. patch 2) than from the less parasitized patch (i.e., patch 1) at the ESS.
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Equation (6) shows that, at the ESS, the dispersal strategies depend only on the prevalences of infestation and the cost of parasitism. They do not depend on the values of the demographic parameters. Although this result cannot be generalized, it suggests that, in a temporally constant environment, the dispersal of individuals does not depend on the life-history traits of the species.

*Temporally varying prevalences of infestation*

When the prevalence of infestation varied temporally and the cost of parasitism was totally compensated for, we found that the selected strategy was always (0.1, 0.1). Thus, the ESSs did not depend on the level of temporal variation (fig. 4). The temporal variations of prevalence homogenize the environment. Fitnesses of parasitized and unparasitized individuals are equal and the probability that one patch had, in the short term, a high prevalence and the other one had a low prevalence is buffered by temporal variation. In these conditions, selection favours an equal proportion of individuals leaving each patch (symmetric dispersal). Individuals should disperse at a low rate. They can thus escape the occasional very bad year.

![Diagram](image)

**Fig. 4.** Evolutionarily stable dispersal strategies in \( m_{12}, m_{21} \) space when parasitized individuals totally compensate for the cost of dispersal. When parasitism rates are temporally constant, the ESSs, represented by the symbol ●, are on the straight line passing through the philopatric strategy. When parasitism rates vary in time, the ESS, represented by the symbol ◦, is always (0.1, 0.1), regardless of the level of temporal variations.
No compensation for the cost of parasitism

Here, the cost of parasitism is not compensated for by an increase in the survival of parasitized adults. Again, we found that the selected dispersal rates depended on the temporal variations in prevalence. When prevalences were temporally constant, two dispersal strategies were selected. When prevalences varied in time, only one dispersal strategy was an ESS. However, in contrast to the previous case, the selected strategy depended on the level of the temporal autocorrelation of prevalence.

- Temporally constant prevalences of infestation

We found that two dispersal strategies were ESSs: (0.1, 0.3) and (0.3, 0.8) (fig. 5). Further, the philopatric strategy (i.e., $m_{21} = m_{12} = 0$) coexisted with any different strategy. At the ESS, $m_{21} > m_{12}$: again, it is more advantageous to leave the site with the highest parasitism rate than the reverse. Further, when $m_{12} = 0.1$ or 0.3, equation (6) shows that movements from patch 2 to patch 1 are higher when the cost of dispersal is not compensated for than when it is. Increasing the dispersal rate when there is no compensation is a mean of reducing the cost of parasitism.

![Graph showing evolutionarily stable strategies](image)

**Fig. 5.** – Evolutionarily stable dispersal strategies in $m_{12}, m_{21}$ space when parasitized individuals do not compensate for the cost of dispersal. When parasitism rates are temporally constant, two different strategies are ESSs (symbol ●). When parasitism rates vary in time, to each value of the standard error SE corresponds a unique ESS (● for SE = 0.1, ■ for SE = 0.5 and ▲ for SE = 0.9). When temporal variations increase, ($m_{12}, m_{21}$) draws near (0.5, 0.5).

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- Temporally varying prevalences of infestation

When prevalences of infestation varied temporally and the cost of parasitism was not compensated for, we found that only one dispersal strategy was selected for each value of the standard error. The corresponding dispersal rates were symmetric (i.e., $m_{23} = m_{12}$). The position of the ESS in $(m_{13}, m_{31})$ space varied with temporal variation (fig. 5). In this case, we observed that, when temporal variability increased, dispersal increased and tended to (0.5, 0.5). While it is true that individuals have interest in preventing a decrease of patch quality, they also have an interest in anticipating an increase. This strategy corresponds to an equal probability of staying in the birthpatch, or leaving it.

Conclusion: Influence of the level of the temporal autocorrelation of parasitism

Our results show that different dispersal strategies are selected when prevalences of infestation follow different patterns of temporal variation. When the environment is temporally constant, asymmetric dispersal rates (i.e., $m_{21} \neq m_{12}$) are ESSs. In that case, the habitat quality determines which dispersal strategies are selected. As would be expected, the proportion of migrants increases when the habitat quality decreases. When the environment is not temporally constant, symmetric dispersal rates (i.e., $m_{21} = m_{12}$) are ESSs. The temporal variation of prevalences buffers the differences between the two patches and selection favours an equal proportion of individuals leaving each patch. The level of temporal variation acts differently depending on the compensation for the cost of parasitism. When the cost of parasitism is totally compensated for, individuals should disperse at a low rate, whatever the level of temporal variation. The dispersal strategies which are selected do not depend on the temporal autocorrelation of the prevalence. When the cost of parasitism is not compensated for, the selected dispersal strategies depend on the level of temporal variation of prevalence. A decrease in the temporal autocorrelation of habitat quality acts to select an increase in the dispersal rates.

The generality of our results is limited by the few values used for the demographic parameters and the step of 0.1 used for the dispersal rates in the simulations. However, we have shown that a dispersal strategy which is favoured in a particular case of temporal variation and level of compensation for the cost of parasitism would be unfavoured in a different context. This result suggests that the temporal dynamics of the factors affecting breeding patch quality could have a strong effect on the dispersal behaviour observed.

PERSPECTIVES ON PATCH QUALITY DYNAMICS, DISPER SAL AND METAPOPULATION FUNCTIONING

We have shown that (1) the factors affecting the quality of breeding habitats vary spatially and temporally and (2) their patterns of variation may affect dispersal behaviour. In this context there is a clear need to consider information on the spatio-temporal dynamics of the factors affecting habitat quality. It may thus be interesting to investigate conditions in which it is rewarding for the individuals to obtain information on the current quality of the breeding patches to be used for future settling decisions. This would depend on environment predictability, which
could be modeled through different patterns of temporal autocorrelation (fig. 3). In this section we propose different empirical and experimental approaches to investigate further the implications of environmental variability of dispersal and recruitment strategies.

**Using an integrative measure of patch quality**

A first important step when working on habitat selection should not only be examining the spatial heterogeneity of the environment, but also its temporal predictability (Switzer, 1993). However, it is often difficult to infer exactly the effects and the spatio-temporal dynamics of the different factors affecting habitat quality. One solution is to focus on the spatio-temporal variations of breeding success itself, without concentrating on the nature of the environmental factors involved. Such investigations carried out at different spatial scales should provide valuable information to be compared to the types of recruitment and dispersal patterns observed. This assumes that individuals present on the different patches show a relatively homogeneous response to the various local environmental factors, so that local reproductive success a given year can be considered as a measure of relative patch quality that year. Such an homogeneous response is not likely to occur (antipredator strategies or susceptibility to parasites might differ with age, experience or genetics of individuals), but this procedure nevertheless provides an integrative way of considering the potential role of each environmental factor on dispersal and habitat selection through their effects on spatio-temporal dynamics of breeding habitat quality. Breeding success can be measured as the average number of offspring fledged per breeding attempt on the patch in a given year, or the proportion of successful breeding attempts.

In the Kittiwake, the temporal autocorrelogram of cliff reproductive success of a large sample of breeding cliffs in two Cape Sizun study colonies for the period between 1982 and 1993 shows that reproductive success was positively autocorrelated between year \( t \) and year \( t + n \) for \( n \leq 3 \) (fig. 6). In the longer

![Temporal autocorrelogram of cliff reproductive success](image)

**Fig. 6.** - Temporal autocorrelogram of the cliff reproductive success in two Kittiwake colonies of the Cape Sizun between 1982 and 1993. Black squares represent significant autocorrelation coefficients (Moran's I) at the 0.05 level. Cliff reproductive success is positively autocorrelated between successive years, but not for time lags longer than three years.
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term, there was no more autocorrelation (fig. 6). This pattern has some similarities with the temporal variations of prevalence of infestation by ticks of the same cliffs. However, the temporal autocorrelogram of prevalence of infestation by ticks shows negative autocorrelations for time lags of several years (BOULINIER et al., unpublished). These differences may result from the dynamics and the interaction of the different factors affecting the breeding success at this scale. Investigations of the temporal variability of breeding habitat quality could thus be carried out on several existing data sets of breeding success, and could be used to test predictions regarding dispersal and metapopulation dynamics.

Developing metapopulation models incorporating habitat selection

Our model of the evolution of dispersal in a simple temporally varying environment compared strategies with fixed proportions of dispersing individuals. The dispersal strategies were not conditional on the value of a given characteristic of the environment at a given time. This approach neglected any process of information gathering prior to settling. However, in animals with sufficient abilities for movement and cognition, settling in breeding patch may actually result from a choice among alternatives (i.e., true habitat selection, WIENS, 1976). In such cases, it could be a good strategy to gather information on habitat quality one year for future settling decisions. We have shown above that the temporal variations of breeding success apparently reflects the temporal variations of the factors affecting habitat quality. In this context, the dispersal and recruitment strategies followed by individuals may rely on the presence or the reproductive success of conspecifics (KLÖPPER & GANZHORN, 1985; REED & DOBSON, 1993; BOULINIER & DANCHIN, in press). A theoretical model of habitat selection which incorporates this behaviour could be compared with the results of our simple model, in which individuals did not use information to select a breeding patch.

Using simple optimality models, it has been recently shown that the use of the presence of conspecific or their reproductive success to select a breeding patch should be selected if the environment is patchy and predictable at the scale at which dispersal occurs (FORBES & KAISER, 1994; BOULINIER & DANCHIN, in press). If patch quality is not predictable from one breeding season to another, habitat selection should not be based on the breeding patch quality of the previous year. In such cases, individuals may distribute themselves in the environment randomly as suggested by our model. The choice may be done in relation to a cue available early in the breeding season, or according to their place of birth or their site of previous reproduction, if knowledge of the area or previous ownership of a site provides advantages. If breeding patch quality is temporally predictable, the fitness of a strategy may depend on the strategies followed by the other individuals in the metapopulation, which underlines the potential for frequency-dependent processes and the need for a game theory approach. In parallel, various density-dependent effects are expected to occur within patches (BROWN et al., 1990). Further theoretical investigations should thus investigate the effect of the shape of density-dependence curves on the type of habitat selection strategy selected. Another important aspect of such an approach would be to determine the consequences of the dispersal strategies selected for the distribution of individuals among patches. In particular, the resulting distribution of individuals among patches could be compared to the one corresponding to an Ideal Free Distribution, as has been done in the context
of optimal foraging (BERNSTEIN et al., 1988). This would allow investigation of the effect of the Ideal Free Distribution's assumption of a perfect knowledge of breeding patch qualities by the individuals as well as a more detailed examination of the effect of such behaviours on the risk of metapopulation extinction (RAY et al., 1991).

**Testing the existence of complex habitat selection strategies**

Depending on the spatial scale and species considered, one may be able to make the working assumption that there is no heterogeneity of survival rate and proportion of non-breeder among breeding patches, and that local reproductive success is mainly affected by the geographic location of the breeding site. In such cases, the local rates of change in the number of breeders provide direct information on the balance of local recruitment and dispersal processes. For species that first breed at a minimum age of 2, this balance can be used to test whether information on breeding patch quality, such as previous year local reproductive success, may have been used in the processes of habitat selection (BURGER, 1982; BOULINIER, 1996; DANCHIN et al., unpublished). These simple demographic analyses could thus be carried out at different scales to test whether different conditional habitat selection strategies occur in temporally predictable habitats.

Nevertheless, the assumption of homogeneous survival rates among breeding patches is not likely to hold in many situations (notably at large spatial scales) and therefore information on the fate of individually marked birds among different patches should be utilized (PRÉVOT-JULLIARD et al., in press; DANCHIN et al., unpublished). In particular, statistical tools are now available to consider both dispersal and survival probabilities (HESTBECK & NICHOLS, 1991; NICHOLS & KENDALL, 1995; SPENDELOW et al., 1995) and could be used to investigate the effect of local factors on dispersal and recruitment among patches, taking into account potentially different survival probabilities among patches (NICHOLS & KENDALL, 1995).

Finally, experiments involving the local manipulation of a potential cue used by the birds should be carried out. Such experiments may be carried out concurrently with management actions (e.g., RENDON MARTOS & JOHNSON, 1996).

**CONCLUSION**

The temporal variability of breeding patch quality needs to be considered when investigating dispersal and metapopulation functioning in birds. Several long-term data sets of different metapopulations are available to carry out such analyses. These should be combined with more detailed studies of the fate of individually marked birds to understand the role of local environmental factors in dispersal. Complementary to these field studies, should be the development of specific theoretical investigations which would incorporate behavioural mechanisms of habitat selection into more realistic metapopulation models and thereby provide testable predictions. Understanding the factors affecting habitat selection among patches should have direct implications for the conservation of species living in fragmented habitats (SMITH & PEACOCK, 1990).
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