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The evolution of informed natal dispersal: inherent versus acquired information

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ABSTRACT

In a predictable environment, variation in quality among breeding sites should select for mechanisms by which animals can increase their chances of ending up in a good site. In this paper, I develop an optimality model that explicitly considers the use of information by first-time breeders for selection of local breeding habitat. The model compares the expected fecundity in the first breeding season of two strategies. One strategy (natal dispersal) allows individuals to prospect (i.e. gather information) for good future breeding sites at a cost that increases with their prospecting activity. Individuals using the other strategy (natal philopatry) have complete information about their natal breeding site at the time of birth and they do not prospect. Allowing prospecting activity and age at first breeding to evolve, the model yields several qualitative predictions about how natal dispersal within a population should evolve under different environmental (prevalence of good sites, predictability of site quality among years) and demographic (pre-breeding survival rate) conditions. Natal philopatry is expected to prevail in all environments when pre-breeding survival is low, while increasing pre-breeding survival should allow natal dispersal to dominate in an increasing range of environments, appearing first in unpredictable environments.

Keywords: age at maturity, habitat selection, information gathering, philopatry, prospecting.

INTRODUCTION

Selecting an appropriate breeding site may play an important role in determining an individual's survival and reproductive success. If the variation among breeding sites causes variation in individual fitness, then selection should favour the evolution of mechanisms to recognize breeding sites of high quality. There are many examples of how individuals move from adverse conditions to good ones (e.g. Ims, 1989; Nilsson, 1989; Thompson and Furness, 1991; Brown and Brown, 1992; Negro *et al.*, 1997). These suggest that individuals are indeed often capable of distinguishing good breeding sites from those of low quality. Furthermore, several studies of birds and mammals suggest that immature as well as mature

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individuals may actively gather information about alternative breeding sites before they start breeding (reviewed for birds by Reed *et al.*, 1999; see also Larsen and Boutin, 1994; Doolan and MacDonald, 1996).

The specific choice of breeding sites of high quality requires that some cue reflects the variation in quality. At one extreme there may be no cue available or it may be too costly to detect. The quality of the breeding site may, for example, be determined by a food supply that does not emerge before the individuals have already started breeding (Orians and Wittenberger, 1991). Furthermore, gathering information (prospecting) may deprive an individual of limited body reserves (Furness and Birkhead, 1984), or imply an increased risk of predation or infection with parasites (Møller and Erritzøe, 1996). Under these circumstances, an individual cannot make a specific choice and may either settle at random or according to some fixed settling rule (Schjørring, 2001). Individuals that are breeding for the first time could, for example, choose to return to the breeding site where they were born. This breeding site is known to have been of good quality in the year of birth, since the individual itself survived being born there (Ashmole, 1962). Natal philopatry could, therefore, provide the individual with a higher probability of obtaining a good breeding site than if settling at random, if the effects of factors determining the quality of breeding sites are predictable from one year to the next (Burger, 1982; Danchin *et al.*, 1998). Analogously, established breeders may use the settling rule of remaining in sites where they have previously bred successfully, while leaving sites where they have already been unsuccessful (Switzer, 1993).

If, on the other hand, the environment does offer some cue that reflects the variation in quality among breeding sites, individuals may benefit from taking this information into account when deciding where to breed. As long as the costs involved do not outweigh the benefits completely, and vice versa, some intermediate optimum sampling activity will exist, at which individuals have some but not complete knowledge about the quality of potential breeding sites.

Thus, when the quality of breeding sites is predictable from one season to the next, individuals could benefit from taking either inherent information (information about the quality of a particular breeding site) or acquired information (information about the quality of a set of breeding sites) into account. The less widespread the good breeding sites, the larger the benefit is expected to be. A high cost of acquiring information should make the use of inherent information a more attractive option. On the other hand, since the predictability of quality between seasons is unlikely to be perfect (Orians and Wittenberger, 1991), the predictability of site quality for first-time breeding individuals will decrease with the time lag between birth and age at first reproduction. This would make the use of acquired information the more attractive option, if age at first reproduction is delayed. Which of the two strategies of information use an individual should follow will thus be linked to factors determining age at first reproduction and the cost of prospecting.

Previous approaches to understanding the evolution of dispersal have either not considered the amount of information as being important for decision making, or they have considered individuals to have either perfect or no information about potential breeding sites, although the gradual evolution of the use of information represents a more plausible scenario. Thus, it is natural to consider a framework in which different amounts of knowledge are possible.

Here, I develop a simple optimality model for the evolution of informed natal dispersal at the local scale within populations, which explicitly considers information gathering as a

continuous process. The model compares the expected fecundity of two strategies differing in the kind of information used to locate breeding sites of high quality. Individuals with one strategy actively gather information while the other strategy relies on inherent information about the quality of the natal breeding site. In particular, I consider how (i) the propensity to disperse, (ii) the prospecting (the process of gathering information) activity and (iii) the age at first breeding are affected by changes in (i) the annual survival rate of individuals, (ii) the predictability of the environment and (iii) the proportion of sites of high quality.

THE MODEL

The model describes the fecundity that an individual can expect in the season when it first attempts to breed, if it follows either an information acquisition strategy (from here on referred to as the ACQ strategy) or a strategy using inherent information without any prospecting (from here on referred to as the INHER strategy).

The environment consists of a large number of breeding sites. A fixed proportion, α, of these is of high quality, while the rest, $(1 - \alpha)$, do not allow successful breeding. The probability of ending up in a site of high quality is thus α if settling is at random. The ACQ strategy can increase this probability by prospecting in the year before breeding starts. The increase in the probability is positively related to the prospecting activity, and will also depend on how predictable the quality of breeding sites is from one season to the next. This predictability, x, can attain values between 0 (no predictability) and 1 (perfect predictability). Thus, for the ACQ strategy, the probability of ending up in a site of high quality is the sum of (1) the probability of choosing a site of high quality on the basis of acquired information that is valid (i.e. correctly predicts the quality) the following season, and (2) the probability of choosing a site of high quality by chance if the acquired information is not valid the following season:

$$f(y)x + [1 - f(y)x]\alpha = f(y)x(1 - \alpha) + \alpha \quad (1)$$

where $0 \leq f(y) \leq 1$ is the information obtained with prospecting activity y. I assume that the information content increases monotonically with prospecting activity to an asymptotic value of 1. This can be modelled with the function $f(y) = (y/(y + k_1))$, where k_1 is a constant determining the prospecting activity at which an individual obtains 50% of the available information.

Individuals using the INHER strategy, on the other hand, settle in their natal site, which was of high quality during the birth season. The probability that the natal site is still of high quality when the philopatric individual starts breeding at age t is the sum of the probability that the information from the birth season is still valid and the probability that the site is of high quality if the information is not valid. Assuming that the validity of information decreases by a constant predictability, x, every year so that it is x^t after t years, this can be written as:

$$x^t + (1 - x^t)\alpha = x^t(1 - \alpha) + \alpha \quad (2)$$

The annual survival rate, β, is assumed to be constant during the pre-breeding period and to be the same for the two strategies. Thus, the probability of surviving to the first breeding attempt at age t is

$$\beta^t \quad (3)$$

Once an individual has selected a breeding site, it must compete for the acquisition of it (Birkhead and Clarkson, 1985). Both strategies have the same probability of acquiring a breeding site and individuals are assumed to compete for sites of high quality. Young individuals may be competitively inferior to older individuals (Potts *et al.*, 1980; Sutherland and Parker, 1985; Arcese, 1989), due to differences in experience, physical strength or status, and they may be less likely to acquire and hold a territory in a contest. The acquisition probability is therefore allowed to increase monotonically with age to the asymptotic value of 1, and is given by:

$$A(t) = \frac{t^{a_2}}{t^{a_2} + k_2{}^{a_2}} \tag{4}$$

where the constant k_2 determines the age at which an individual has a 50% chance of acquiring the breeding site and a_2 determines the slope of the increase in the acquisition probability at this point.

The prospecting activity of the ACQ strategy is assumed to imply a cost that increases with the level of prospecting. Prospecting may necessitate migration to the breeding areas, and higher densities of individuals in these areas may expose prospectors to higher levels of aggression (Arcese, 1989), competition for food (Furness and Birkhead, 1984) or pathogen transmission (Møller and Erritzøe, 1996) than they would otherwise have experienced. This cost may be expressed as decreased survival or reproduction. The model makes no assumptions about the kind of cost involved. However, it does assume that the cost only affects the expected fecundity in the first breeding season of the individual. So that the function defining the cost is consistent with the probability terminology of the model, the cost is represented by the following logistic function:

$$C(y) = \frac{y^{a_3}}{y^{a_3} + k_3{}^{a_3}} \tag{5}$$

where k_3 is a positive constant determining the prospecting activity at which the expected fecundity at first breeding is reduced by 50% and a_3 is a positive constant determining the slope of the decrease in expected fecundity at this point.

The expected fecundity at first breeding, r, is obtained by multiplying the component probabilities:

$$r_{\mathrm{ACQ}}(y, t) = \left[\left(\frac{y}{y + k_1}\right)x(1 - \alpha) + \alpha\right] A(t)[1 - C(y)]\beta^t \tag{6}$$

for the ACQ strategy, and

$$r_{\mathrm{INHER}}(t) = [x^t(1 - \alpha) + \alpha]A(t)\beta^t \tag{7}$$

for the INHER strategy. Note that the two strategies converge with a strategy of random settling when the predictability, x, is close to zero or the proportion of good sites, α, is close to 1.

The individuals are assumed to seek maximization of their expected fecundities. Age and prospecting activity, therefore, attain the values that maximize the expected fecundity under the given conditions. However, age was constrained to attain only integer values.

From the model (equations 6 and 7), I calculated the expected fecundities of the prospecting ACQ strategy and the INHER strategy for different values of predictability, x, proportion of good sites, α, and annual survival, β, representing the whole range of possible values. The constants in the model were assigned values that would allow some variation to occur when varying the independent variables. However, the qualitative predictions of the model were robust to changes in the particular shapes of the probability functions as long as their monotonical properties were unchanged.

When presenting and discussing the results of the model, I make use of the terms 'level' and 'value' of information. The level of information is the extent to which individuals are able to correctly identify breeding sites of high quality at a given age. It is thus equivalent to $f(y)x$ (equation 1) for the ACQ strategy and x^t (equation 2) for the INHER strategy. The value of information, on the other hand, is the extent to which the use of information increases an individual's expected fecundity above that of an individual settling at random. The value is thus equivalent to $x(1-\alpha)$ (equation 1) for the ACQ strategy and $x^t(1-\alpha)$ (equation 2) for the INHER strategy.

RESULTS OF THE MODEL

The two strategies for habitat selection involve several critical trade-offs that determine the optimal age at first breeding, the optimal prospecting activity and, ultimately, which of the two strategies will have the higher expected fecundity.

The ACQ strategy trades information for body condition by varying prospecting activity. This means that, when the additional information obtained by prospecting has a high value (i.e. gives a large increase in expected fecundity), prospecting activity should be high with a simultaneous high cost. Gathering additional information will be particularly valuable when the prevalence of breeding sites of high quality is low, and the predictability of site quality from one season to the next is high (Fig. 1). Another trade-off for the ACQ strategy is the one between survival and site acquisition by varying age at first breeding. When the annual survival rate increases, the mortality cost of increasing age at first breeding decreases, and the higher probability of acquiring a breeding site at older age will cause the optimal age at first breeding to increase (Fig. 2a).

The INHER strategy trades survival and information for the probability of acquiring the desired breeding site by varying age at first breeding. Thus, as for the ACQ strategy, age at first breeding increases when the annual survival rate increases, although at a lower rate than for the ACQ strategy because of the additional cost of the devaluation of information (Fig. 2b–e). This cost of devalued information will be largest, and the increase in age at first breeding therefore smallest, when the proportion of good sites is low and the predictability of quality between seasons is of intermediate values (Fig. 2c–e). When the proportion of good sites is low, information is very valuable, because the probability of randomly settling in a low-quality site is high. The devaluation of information over time is highest when the predictability is of intermediate values. When the predictability is low, the value of the information is very low, since the quality of a site in one season is a poor predictor of its quality in the next. On the other hand, when the predictability is very high, the value of the information is high, not only from one season to the next, but also over longer time periods, and the devaluation of information over time is therefore low under these conditions.

In the model, the ACQ strategy cannot achieve a higher expected fecundity than the

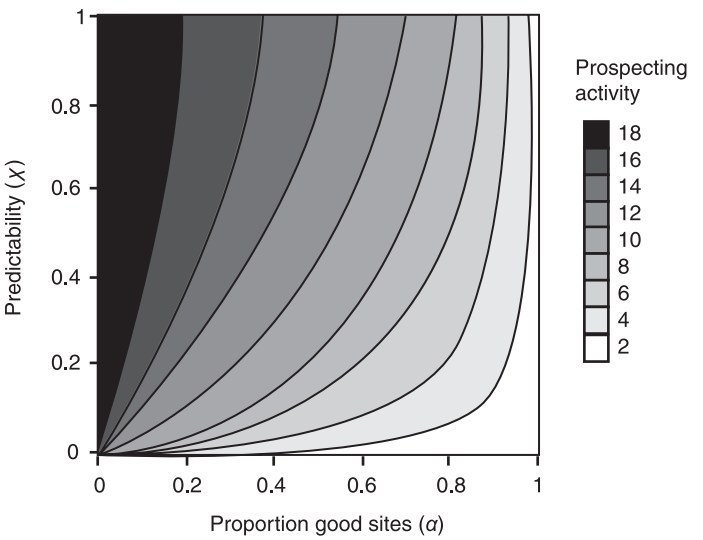

Fig. 1. Optimal prospecting activity of the ACQ strategy in relation to the proportion of breeding sites of high quality (habitat quality), α, and the predictability of the quality of breeding sites between years, x. $k_1 = 5$, $k_2 = 1$, $k_3 = 50$, $a_2 = 2$, $a_3 = 2$. The constants are defined in the text.

INHER strategy as long as the optimal age at first breeding is 1, that is at low survival rates (Fig. 3). Even with a very high prospecting activity ($y/(y + k_1) \approx 1$), allowing the ACQ strategy to obtain the same level of information as the INHER strategy, any cost of prospecting will cause the expected fecundity of the ACQ strategy to be smaller than that of the INHER strategy. If the survival rate is high enough to make it advantageous for the ACQ strategy to increase the age at first breeding, the ACQ strategy will have a higher expected fecundity than the INHER strategy under some circumstances.

As long as the optimal age of the INHER strategy is 1, and that of the ACQ strategy is just slightly higher (Fig. 2a and 2c), the level of information of the INHER strategy will be better than that of the ACQ strategy, and the ACQ strategy can only persist when the value of information is low – that is, when the proportion of good sites is high or the predictability of site quality between seasons is very low (Fig. 3b). However, as the survival rate increases, the ACQ strategy will increase its expected fecundity further by increasing the age at first breeding (thereby increasing its chances of acquiring a breeding site), eventually outweighing the INHER strategy's advantage of a higher information level (Fig. 2a,d,e, Fig. 3c,d).

Under circumstances favouring an increase in age at first breeding for the INHER strategy (i.e. high prevalence of good sites and/or very low or very high predictability of site quality between seasons; Fig. 2c), the ACQ strategy is able to achieve a higher level of information by prospecting than the INHER strategy when the predictability of site quality is intermediate to low and the prevalence of good sites is intermediate to low (Fig. 3b). However, if the predictability is high, the INHER strategy will have a higher expected fecundity, because of the small devaluation of information with age and the ACQ strategy's additional cost of prospecting (Fig. 1, Fig. 3b). Furthermore, if the prevalence of good sites is very high,

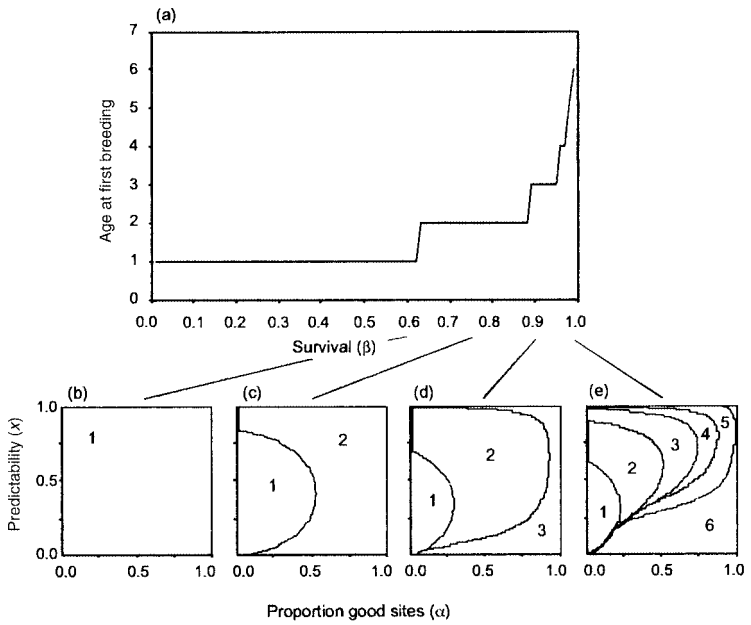

Fig. 2. Optimal age at first breeding in relation to annual pre-breeding survival rate, β, for the ACQ strategy (a). In addition to β, the optimal age at first breeding for the INHER strategy depends on the proportion of breeding sites of high quality (habitat quality, α, and the predictability of the quality of breeding sites, x). Thus, for the INHER strategy, the optimal age at first breeding is shown in relation to α and x for selected values of β: (b) ≤ 0.60, (c) 0.75, (d) 0.90 and (e) 0.99. The contour lines separate areas where the different ages are optimal. The optimal age within a given area is indicated. The constants have the same values as in Fig. 1.

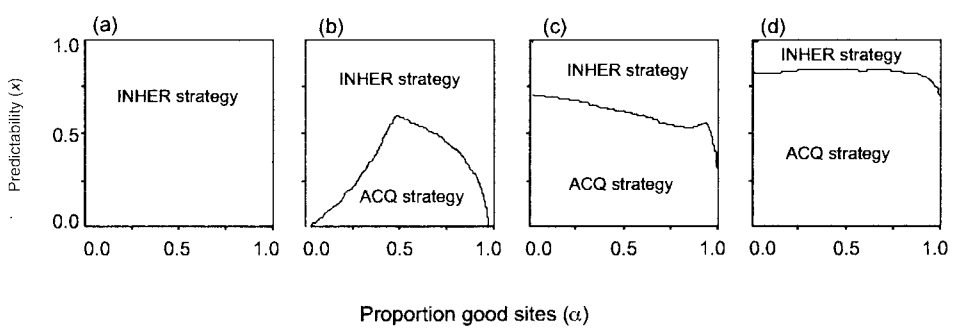

Fig. 3. Optimal habitat selection strategy in relation to the proportion of breeding sites of high quality (habitat quality), α, and the predictability of the quality of breeding sites between years, x. The results are shown for four different levels of the annual pre-breeding survival rate, β: (a) ≤ 0.60, (b) 0.75, (c) 0.90 and (d) 0.99. The constants have the same values as in Fig. 1.

the value of information is very small, so that the ACQ strategy will be inferior to the INHER strategy due to the cost of prospecting (Fig. 1, Fig. 3b). With a further increase in survival rate, which causes a larger difference in age at first breeding between the two strategies, the

INHER strategy can expect a higher fecundity only when the predictability of site quality is very high (Fig. 3c,d).

DISCUSSION

The optimality model developed here yields several qualitative predictions for conditions under which either use of acquired or inherent information should be the optimal strategy for habitat selection of individuals breeding for the first time. In contrast to previous approaches, the process of information gathering is explicitly considered, allowing the level of information to take on continuously varying values.

In the model, an individual's choice of its habitat selection strategy is determined by the fecundity that it can expect to obtain in its first breeding season. The ACQ strategy allows an individual to collect information about the quality of prospective breeding sites before it starts to breed. Obtaining this information, however, implies a cost that increases with the level of prospecting activity. Individuals using the INHER strategy, on the other hand, have complete information about the natal breeding site at the time of birth, and they do not perform additional sampling of the breeding environment before the start of breeding. Both strategies provide the same probability of acquiring a given breeding site, a probability that increases with age.

Although individuals with an ACQ strategy may end up settling in their natal breeding site if it remains of high quality and thus enters the set of chosen sites, this strategy will in general result in natal dispersal within populations, while the INHER strategy will consistently lead to natal philopatry.

The model predicts that natal dispersal should be more common and age at first breeding higher in populations with a high survival rate before sexual maturity than in those with a low survival rate (Figs 2 and 3). Natal philopatry should be more prevalent in highly predictable habitats than in more unpredictable ones (Fig. 3). For species with intermediate levels of survival rates before sexual maturity, natal philopatry should also be found in habitats of low predictability under conditions with either a low or high proportion of good sites (Fig. 3). However, when the predictability of quality is low, the benefit of using an information-based selection strategy as compared to settling at random is very small. The prospecting activity of the ACQ strategy is expected to increase with the predictability of site quality and decrease with the proportion of good sites (Fig. 1). Thus, when breeding sites of high quality are rare, and when the predictability between years is high, the level of prospecting is expected to be high.

Assumptions of the model

The assumed effect of age on the probability of acquiring a breeding site is crucial for the predictions of the model. Without this effect, the optimal age at first breeding would always be 1 for both strategies, and the INHER strategy would always be superior to the ACQ strategy, because of the latter's additional cost of prospecting. Thus, the expected fecundity of the ACQ strategy can only exceed that of the INHER strategy when delayed breeding is favoured, since the value of information decreases for the INHER strategy but not for the ACQ strategy when age at first breeding increases.

In the model, the optimal age at first breeding is set by the trade-off between survival, level of information and the probability of acquiring a breeding site. It is probable that

additional factors and trade-offs affect the age at first breeding observed in real populations. An increase in adult mortality with increasing population density, for example, could cause the optimal age at first breeding to increase (Stearns and Koella, 1986). On the other hand, in rapidly increasing populations, the advantage of a shorter generation time could make an earlier breeding start advantageous (Charlesworth, 1980). Moreover, mate acquisition and foraging ability have also been hypothesized to constrain an early start to breeding in some cases (Marchetti and Price, 1989). The objective of my model, however, is not to explain the evolution of delayed breeding, but rather to allow some age-dependent dynamics to be represented in the model to investigate how the simultaneous evolution of age at first breeding may affect the evolution of habitat selection strategies and vice versa. Since the value of information is strongly dependent on the time lag between its acquisition and its use, the dynamics of informed habitat selection and a delayed start to breeding are closely linked.

In their optimality model for the evolution of a prospecting strategy, Boulinier and Danchin (1997) concluded that such a strategy would have a higher lifetime reproductive success in comparison to a random settling strategy under conditions of high survival, high predictability of site quality between years and low prevalence of breeding sites of high quality. Prospecting activity and age at first breeding were not allowed to evolve in their model, and the prospecting strategy was assumed to pay the cost of delaying age at first breeding by one season. In the more general model presented in this paper, prospecting activity is allowed to evolve, and the random strategy is thus a special case of the prospecting strategy where prospecting activity is equal to zero. However, results similar to those of Bouliniers and Danchin (1997) also emerge from the model presented here, as the optimal prospecting activity is predicted to be very high when the predictability of site quality is high and the prevalence of good sites is very low, while prospecting activity should be very low (equalling the random strategy in Boulinier and Danchin, 1997) when the predictability is low and the prevalence of good sites is high.

Contrary to the model of Boulinier and Danchin (1997), the optimal age at first breeding is not constrained by prospecting in the model presented here. It may not always be reasonable to assume that age at first breeding is unconstrained. In animals where pre-breeders cannot prospect in the season of their birth and information about site quality is available only at the end of the breeding season, prospecting may imply a delay of first breeding for at least one season (Boulinier *et al.*, 1996). However, this constraint does not change the predictions of the model with respect to optimal strategy, since the ACQ strategy can never be superior to the INHER strategy when its optimal age at first breeding is 1.

The power of the model to predict the dispersal behaviour of first-time breeders will depend on how strongly this behaviour is determined by the quality of prospective breeding sites. Kin relationships, for example, can have a strong effect on where first-time breeders choose to settle. Direct and indirect fitness costs from inbreeding depression and kin competition favour dispersal behaviour (Hamilton and May, 1977; Pusey, 1987; Ronce *et al.*, 1998; Wheelwright and Mauck, 1998), while benefits from cooperative behaviours between kin favour philopatric behaviour (Watson *et al.*, 1994). In general, the quality of the breeding site is expected to have a strong effect on habitat selection strategies, if it is a major determinant of an individual's fecundity.

Furthermore, prospecting is modelled as a continuous process where information is acquired simultaneously for all breeding sites within a population. The model, therefore, applies best to species where individuals within a population tend to breed close together, as

is the case in colonially breeding species, for example. For species where breeding sites are more scattered, it might be more appropriate to model acquisition of information as a sequential process.

Implications of information-based habitat selection strategies

That individuals use information to select their local breeding habitats may have interesting implications for the population dynamics. Successful founding of new populations from small initial sizes, for example, should be more likely if first-time breeders base their selection of breeding sites on information rather than randomly. With the information-based strategy, they would be more likely to breed successfully in their first attempt, causing the average breeding success and thereby the growth rate of the population to be higher than would have been the case with a random strategy. Furthermore, Ruxton and Rohani (1999) suggest that, in spatially structured populations, information-based habitat selection may stabilize population dynamics, even when the intrinsic dynamics are highly unstable. Information-based habitat selection strategies could thus make populations less likely to go extinct.

Information-based strategies of local habitat selection could furthermore interact with evolutionary processes that depend on the spatial structure of local populations, such as the evolution of cooperative behaviour through kin selection. Conditions favouring philopatry of first-time breeders (i.e. high predictability; Fig. 3) are also likely to favour fidelity of established breeders to their former breeding sites (Switzer, 1993, 1997), especially when good breeding sites are rare (due to the cost of locating them). This would result in parents and offspring breeding near one another, which would facilitate the evolution of cooperative interactions among neighbours through kin selection (Hamilton, 1964, 1972; Greenwood, 1980). The evolution of such interactions would, in turn, affect the evolution of habitat selection by adding a benefit to philopatry (Stacey and Ligon, 1991).

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