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Evolution of heterospecific attraction: using other species as cues in habitat selection

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Abstract. We analyzed the ecological conditions that may favor a habitat selection process in which later arriving individuals (colonists) use the presence of earlier established species (residents) as a cue to profitable breeding sites (heterospecific attraction). In our model, colonists assessing potential breeding patches could select between high-quality source and low-quality sink patches. A proportion of the source patches were occupied by residents. Colonists could either directly sample the relative quality of the patches (termed samplers) or, alternatively, they could also use residents as a cue of patch quality (cue-users). Cue-users gained benefit from lowered costs when assessing occupied source patches. The cue-using strategy is an efficient way to choose the best possible patch not only when interspecific competition is intense, but also when benefits from social aggregation exceed the effects of competition. High relative cost of sampling empty patches increases the fitness of the cue-using strategy relative to samplers. The strongest attraction to heterospecifics was predicted when the benefit from aggregating with residents exceeded the effects of competition, and approximately half of the landscape consisted of occupied, high-quality source patches.

Key words: analytic modeling, colonists, habitat selection, heterospecific attraction, landscape composition, residents

Introduction

'Heterospecific attraction' was coined by Mönkkönen et al. (1990) to describe the situation where individuals choose habitat patches by the presence of established individuals of a heterospecific species (residents). Heterospecific cues may be profitable if residents reflect the relative quality of patches or if heterospecific aggregations enhance foraging efficiency or reduce predation risk. The alternative – sampling a patch directly for its relative quality (abundance of predators, food, and other resources) – will take time and consume energy (see Danielson, 1991). If time is a limiting factor in reproduction, later-establishing species may gain advantage by using residents as cues. Numerous empirical studies suggest that heterospecific attraction is a common process, at least in birds (Timonen et al., 1992; Mönkkönen et al., 1996; Elmberg et al., 1997; Mönkkönen et al., 1997; Forsman et al., 1998a, 1998b). So, it is important to determine the ecological conditions favoring heterospecific attraction.

Heterospecific attraction will be an evolutionary stable strategy (ESS) for two species that are potential competitors only if the benefits of selecting patches occupied by another species exceed costs. The ESS requirement will be easiest to satisfy when the costs of assessing habitat suitability are high. The costs are likely to vary with landscape composition (e.g., relative amount of source and sink patches) and the abundance of resident species. In this article, we analyze how competition and the benefits gained from social aggregations and from using other species as cues affect the fitness of colonizing individuals. We also study how landscape composition and the abundance of resident species influence fitness and the potential evolutionary advantage of heterospecific attraction.

The model

We define the *landscape* as a large area within which habitat patches are embedded. A *habitat* is a combination of biotic and abiotic factors that make a certain patch more or less suitable for a species. *Patches* are areas smaller than the landscape that contain only habitat of a single type that fulfill the requirements of an individual. We assume that landscapes are composed of three different habitat types: source habitat patches where reproduction exceeds mortality, sink habitat patches where mortality exceeds reproduction, and matrix that cannot be occupied (Danielson, 1992). We assume that our colonizing organism is a good disperser with good cognitive abilities so that the dilution effects of matrix can be ignored.

We consider here the consequences for a colonizing species from interactions with a resident species. The resident species samples the landscape, settles and may start breeding before the arrival of the colonist species. The two species recognize the same source and sink habitats. Patches for the later arriving species can be further divided into those occupied and those unoccupied by the earlier-establishing (resident) species. We assume that resident populations are regulated by winter conditions to levels well below the summer carrying capacity of the environment, and that residents always settle in the source habitat patches so that their presence reliably reflects habitat quality.

Colonists encounter source patches unoccupied by a resident (u-patches), source patches occupied by a resident (o-patches), and sink patches (s-patches), with relative frequencies p, q and r, respectively, in the landscape. The quality of these three types, as measured by the expected patch-specific fecundity, are denoted B_u, B_o and B_s, respectively. We assume that B_s is always lower than B_u and B_o. The relation between B_o and B_u depends on the intensity of competition.

If the cost of competition exceeds the benefits gained by settling in o-patches (richer food, lower predation, benefits from social aggregation) then $B_u > B_o$, otherwise $B_u < B_o$.

We compare two strategies of sampling the landscape by the colonizing species. Strategy 1: Individuals directly sample food resources and predation risk in order to estimate the relative quality of the patches (termed samplers, hereafter). Strategy 2: individuals also use residents as a quality cue (cue-users). Both strategies impose a fitness cost which lowers the fitness that could otherwise be achieved at the selected patch. The cost may arise, for example, from the time delay in the start of breeding (see e.g., Harvey et al., 1985). Samplers incur a cost C_d for each time unit spent sampling a patch. Cue-users incur the cost C_r, in an occupied patch or C_d if the patch is unoccupied. We assume $C_r < C_d$ because using cues takes less time. Traveling costs between patches are the same for both strategies, and they are not parameterized separately.

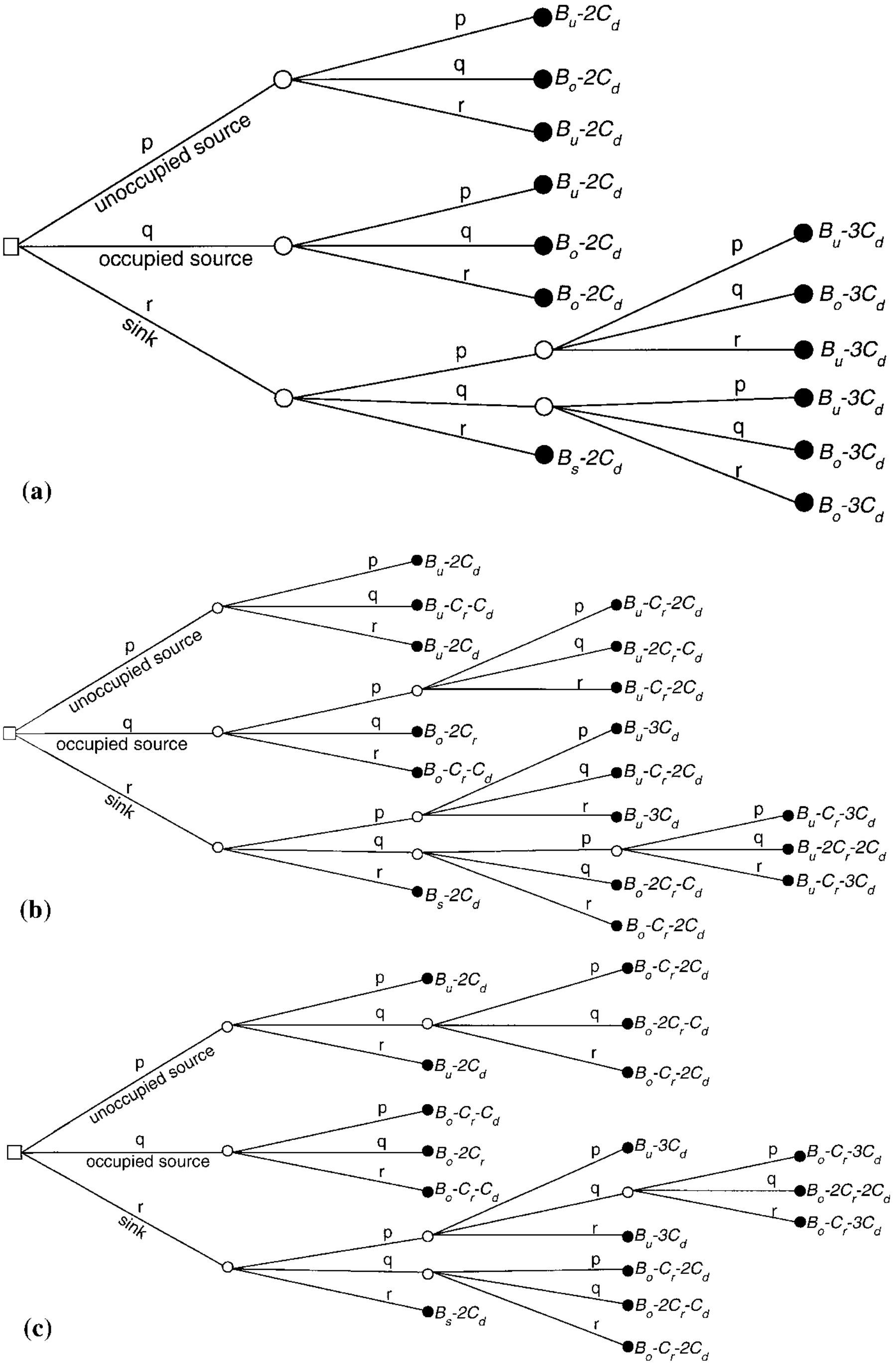
Animals may exhibit various tactics when selecting among patches (see e.g., Janetos, 1980; Wittenberger, 1983). We assume they use a sequential-comparison tactic (SCT). In SCT, animals follow the following rules:

1) Sample at least two patches.
2) Continue to sample if the current patch is better than the previous one.
3) If the current patch equals the previous one, stop and select the current patch.
4) If the current patch is poorer than the previous patch, return and select the former patch.

To analyze the fitness consequences of such a rule, we use a variant of natural decision theory (Cooper, 1981; Cooper and Kaplan, 1982) where sequences can be depicted with decision tree diagrams (Fig. 1) for both $B_u > B_o$ and $B_u < B_o$. Samplers do not assess competition nor benefits by residents, and, therefore, their decision tree is independent of the relation between B_u and B_o. SCT should be advantageous when their risk is high of being pre-empted from the best patches (Wittenberger, 1983). As the selection tactic may have a profound effect on the results, it is important to consider the alternatives. We do this in another paper (Forsman et al., in prep.).

Our model of habitat selection is similar to the ideal pre-emptive distribution of Pulliam and Danielson (1991). As in that model, potential breeding patches differ in expected reproductive success, and a patch occupied by a conspecific is no longer available. Occupation does not influence the expected reproductive success of any other patches. Our model does not result in an ideal distribution because colonists do not necessarily end up selecting the best available patch but rather the best of the evaluated ones.

The fitness equations flow from Figure 1. Going from left to right in the figure, we see that each move to a new patch u, o or s is associated with a probability value p, q, or r dependent on the proportion of each patch type in


(a)
p
unoccupied source
q
occupied source
r
sink
p
B_u-2C_d
q
B_o-2C_d
r
B_u-2C_d
p
B_u-2C_d
q
B_o-2C_d
r
B_o-2C_d
p
B_u-3C_d
q
B_o-3C_d
r
B_u-3C_d
p
B_u-3C_d
q
B_o-3C_d
r
B_o-3C_d
r
B_s-2C_d
(b)
p
unoccupied source
q
occupied source
r
sink
p
B_u-2C_d
q
B_u-C_r-C_d
r
B_u-2C_d
p
B_u-C_r-2C_d
q
B_u-2C_r-C_d
r
B_u-C_r-2C_d
q
B_o-2C_r
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B_o-C_r-C_d
p
B_u-3C_d
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p
B_u-C_r-3C_d
q
B_u-2C_r-2C_d
r
B_u-C_r-3C_d
q
B_o-2C_r-C_d
r
B_o-C_r-2C_d
r
B_s-2C_d
(c)
p
unoccupied source
q
occupied source
r
sink
p
B_u-2C_d
q
r
B_u-2C_d
p
B_o-C_r-2C_d
q
B_o-2C_r-C_d
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B_o-C_r-2C_d
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B_o-C_r-C_d
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B_u-3C_d
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B_o-2C_r-2C_d
r
B_o-C_r-3C_d
r
B_u-3C_d
p
B_o-C_r-2C_d
q
B_o-2C_r-C_d
r
B_o-C_r-2C_d
r
B_s-2C_d

the landscape. The fitness of an individual when each possible selection sequence has stopped is also given in Figure 1. Deriving the fitness equations of the strategies can be described as a left to right process of "averaging out" the fitness consequences of all possible selection routes (Cooper, 1981). For example, if an organism is able to use the presence of residents as a cue (Fig. 1B) and first finds an *u*-patch, the decision rule implies that it is certain to end up settling in this patch type. Thus, it will gain the fitness benefit B_u. The fitness cost for assessing will be C_d (for assessing the first *u*-patch) plus the *average* cost of assessing the second patch, where we must consider the probability of finding each of the possible patches. The expected fitness is therefore $(B_u - C_d - pC_d - qC_r - rC_d)$. Following this logic for all of the possible decision routes, we end up with the fitness equations shown in the appendix.

From the fitness equations, we can derive the conditions for cue-users to have higher fitness than samplers, assuming p, q, and r all ≥ 0 (see Appendix for details). If $B_u > B_o$ then the condition is,

$$C_r < \frac{(1 + q + pq)C_d + p(B_u - B_0)}{qp + q + p + 1} \qquad (1)$$

and if $B_u < B_o$ then the condition is

$$C_r < \frac{(1 + q + pq)C_d - p(B_u - B_0)}{qp + q + p + 1} \qquad (2)$$

That is, the strategy that maximizes fitness is determined by the relationship between C_d and C_r, the intensity of competition in relation to benefits of social aggregations $(B_u - B_o)$ and the composition of the landscape (frequencies p and q). To understand how each of these factors influences fitness of the individuals with different strategies of sampling the landscape, we graphically analyse these conditions and the fitness equations, looking particularly for parameter values where the optimal strategy changes.

Results

All other things being equal, intense competition (large positive value of $(B_u - B_o)$ in Condition 1 or large benefits (large negative value of $(B_u - B_o)$ in Condition 2 increase the fitness of cue-users relative to samplers (Fig. 2). Even

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Figure 1. Decision tree diagram for (a) samplers, (b) for cue-users when $B_u > B_o$ (competition), and (c) for cue-users when $B_u < B_o$ (benefit). The square in the left is the base node where the decision starts. Each move to another patch (to the right from this starting point) is associated with probability p, q or r. Open circles denote states where the decision sequence continues and filled circles denote when the sequence stops. The fitness of an individual when each possible selection sequence has stopped is also given in the end of each branch of the tree.

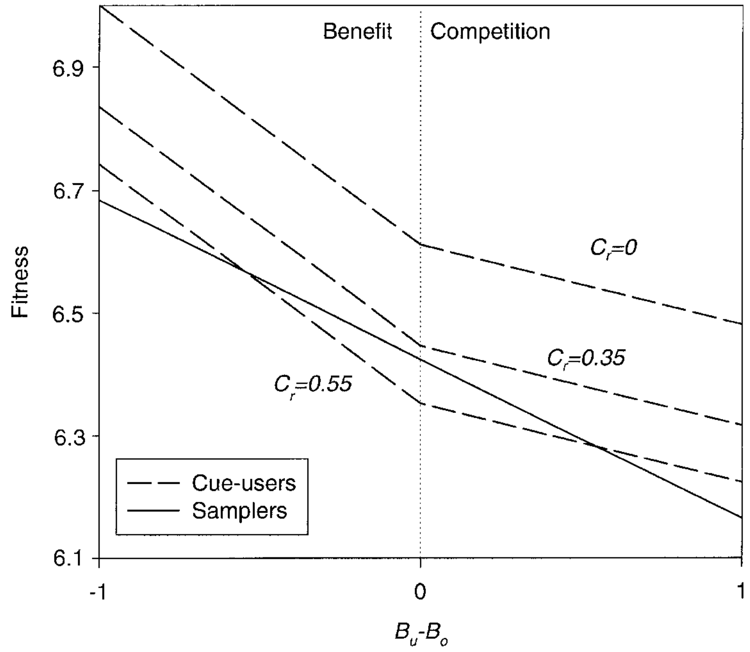

Figure 2. Fitness of cue-users and samplers in relation to the difference in quality between B_u and B_o. When $B_u - B_o$ is negative, the benefits of selecting *o*-patches exceed any costs of competition, and when $B_u - B_o$ is positive competition is more important than benefits. The graph was drawn for the values: $p = 0.5$, $q = 0.2$, $r = 0.3$, $C_d = 0.55$, $B_s = 4$, $B_u = 8$. We let B_o vary from 7 to 9. We calculated fitness curves for cue-users for three different values of C_r exemplifying the fitness effects of cost difference between cue-users and samplers.

at very moderate differences in quality between *u*- and *o*-patches, it is always beneficial to use residents as cues to high quality patches.

If there is no effect of competition and no benefits ($B_u = B_o$), the Conditions 1 and 2 change into

$$\frac{C_r}{C_d} < \frac{1 + q + pq}{qp + q + p + 1} \tag{3}$$

This condition implies that high relative cost of sampling empty patches ($C_d \gg C_r$) increases the fitness of cue-users relative to samplers (fig. 2). The right-hand-side expression ranges between 0.5, when $p = 1$ and $q = 0$, and 1, for all q when $p = 0$. That is, if the cost of assessing a patch by using cues is less than half of the cost of direct sampling of the patch, it is always beneficial to use cues, even if there is no difference in quality between *u*- and *o*-patches. If the cost of using cues equals the cost of direct sampling, it is never beneficial to use cues if there is no additional effect of patch quality difference (i.e. $B_u \neq B_o$).

It follows from Conditions 1 and 2 that the optimal strategy will depend on p and q. If $B_u > B_o$ there will be a change in optimal strategy when

$$C_r = \frac{(1 + q + pq)C_d + p(B_u - B_0)}{qp + q + p + 1} \tag{4}$$

If $B_u < B_o$ there will be a change in optimal strategy when

$$C_r = \frac{(1 + q + pq)C_d - p(B_u - B_0)}{qp + q + p + 1} \tag{5}$$

The quality of the sink patches (B_s) has no influence on whether a cue-using or a direct sampling strategy should be used. This is because assessing sink patches is equally costly for both strategies, and any term containing B_s is averaged out when deriving Conditions 1 and 2 from the fitness equations (see appendix). In the limiting case when there are no occupied source habitat patches ($q = 0$) in the landscape, cue-users and samplers have equal fitness, because the animals will follow the same selection paths independent of strategy (Fig. 1). When the frequency of occupied patches (q) is relatively low, a combination of patch frequencies can be found where it may be more beneficial not to use residents as cues to source patches (hatched area Fig. 3). As the frequency of occupied patches increases, at some point it will become more beneficial to be a cue-user. The location of this value depends on the effect of competition and the difference between C_d and C_r. When there are only sink habitat patches and occupied source habitat patches in the landscape ($p = 0$) it is always beneficial to use cues; Conditions 1 and 2 become $C_r < C_d$ if $p = 0$, which is true by definition. The area of frequencies of q and p when cue-using strategy is best increases with increasing difference in quality between *u*- and *o*-patches (compare rows in Fig. 3) and with increasing difference between C_d and C_r (compare columns in Fig. 3).

The fitness of cue-users is a nonlinear function of q, the proportion of occupied source patches (Fig. 4). The rate of change of fitness and the shape of the curve are determined by the relation between the costs ($C_d - C_r$), and the level of competition ($B_u - B_o$). With no competition or benefit ($B_u = B_o$), sampler fitness is independent of q (Fig. 4). In this case, samplers fitness may be higher than that of cue-users provided that the cost difference is small. More often than not, an increase in q results in an increase in the fitness of cue-users (Fig. 4).

From the decision trees in Figure 1, we can also calculate the probability that a colonist individual selects an *o*-patch. For samplers it is

$$q(p + q + r + pr + qr + r^2) \tag{6}$$

For cue-users if $B_u > B_o$,

$$q(q + r + qr + r^2), \tag{7}$$

and if $B_u < B_o$,

$$q(1 + p + pr + r). \tag{8}$$

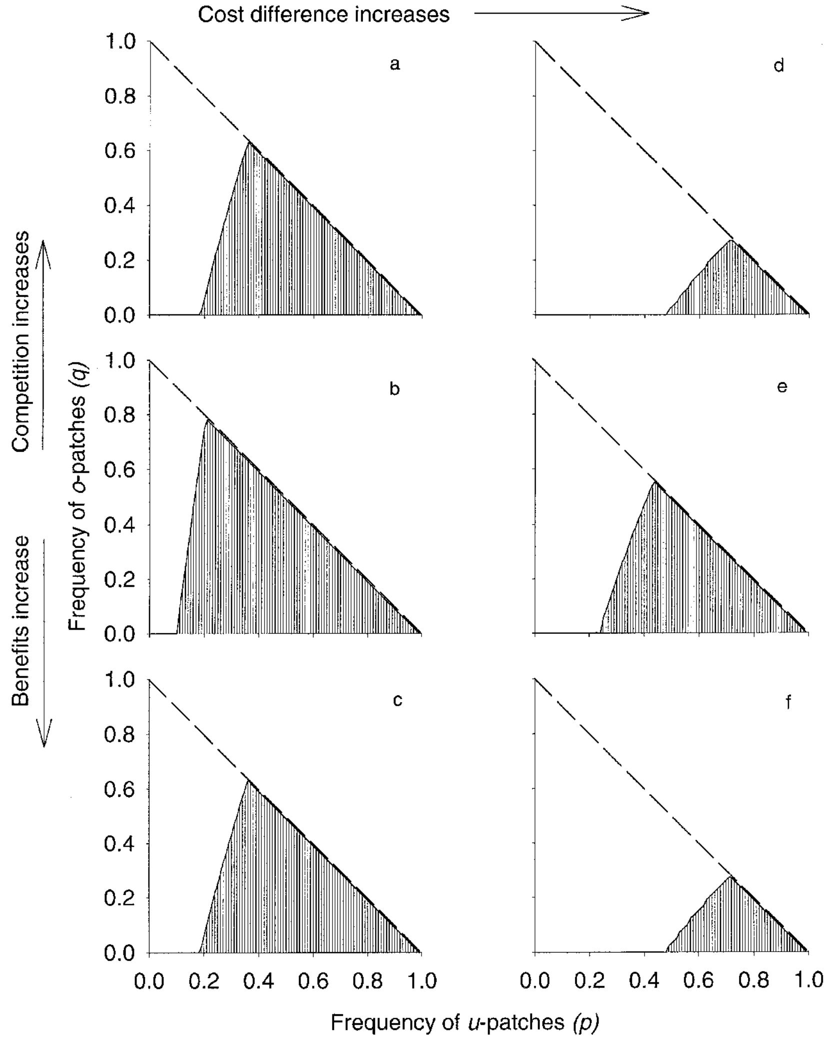

Figure 3. Frequency areas of p, q, and r where the conditions of higher fitness for cue-users than for samplers (see Condition 1 and Condition 2) either hold (open area) or do not hold (hatched area) true. Rows in the figure denote different levels of species interactions, from competition on top to benefit on the bottom, while cost difference increases from the left to the right column. All frequency combinations of p, q, and r can be found to the left of the dashed line. a) $B_u = 8$, $B_o = 7.8$, $C_d = 0.5$, and $C_r = 0.45$, b) $B_u = B_o = 8$, $C_d = 0.5$, and $C_r = 0.45$, c) $B_u = 7.8$, $B_o = 8$, $C_d = 0.5$, and $C_r = 0.45$, d) $B_u = 8$, $B_o = 7.8$, $C_d = 0.5$, and $C_r = 0.4$, e) $B_u = B_o = 8$, $C_d = 0.5$, and $C_r = 0.4$, and f) $B_u = 7.8$, $B_o = 8$, $C_d = 0.5$, and $C_r = 0.4$.

Hence, if $B_u > B_o$ and $p > 0$, a sampler is always more likely to select o-patches than a cue-user (Fig. 5). If $B_u < B_o$ and $p > 0$ then cue-users always have a higher probability of selecting o-patches than do samplers (Fig. 5). A cue-users'

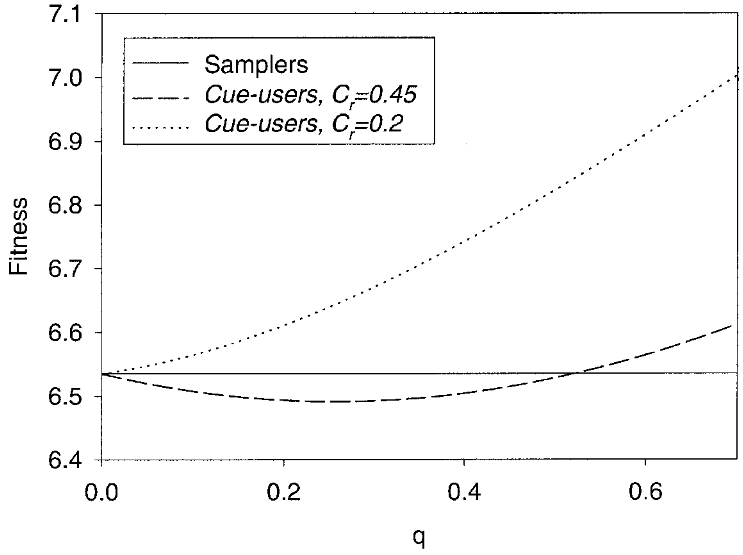

Figure 4. Fitness of cue-users and samplers in relation to the frequency of occupied source habitat, q. The graph was drawn for the values: $r = 0.3$, $C_d = 0.5$, $B_u = 8$, $B_o = 8$, and $B_s = 4$. Because there is no competition nor benefit, samplers' fitness (solid line) does not change with q. For cue-users, the dotted line shows the fitness when $C_r = 0.2$, and dashed line shows the fitness when $C_r = 0.45$.

probability of selecting o-patches is highest relative to that of samplers when $p = q = 0.5$ and $r = 0$.

Discussion

Recognizing the presence of a heterospecific individual seems to be the favored strategy in most cases. Samplers can achieve higher fitness than cue-users only if the difference in quality between occupied and unoccupied source patches is low, and the cost of assessing patch quality directly is low. The advantage to samplers is highest in a landscape with a low proportion of occupied source patches. Then, the relatively more complicated patch selection procedure of cue-users creates costs which override the benefits of avoiding the direct assessment of the patch quality. As can be seen from the decision trees in Figure 1, a cue-user usually assesses more patches before settling, and although some of the patches are comparatively cheap to assess, the higher number of patches can make this strategy less beneficial. We conclude that selection generally favors individuals capable of using other species as cues.

Recognizing the presence of a competitor, i.e., the cue-using strategy, is favored almost irrespectively of the intensity of competition. Why? Because the colonist species is time constrained and has limited ability to find the ideal

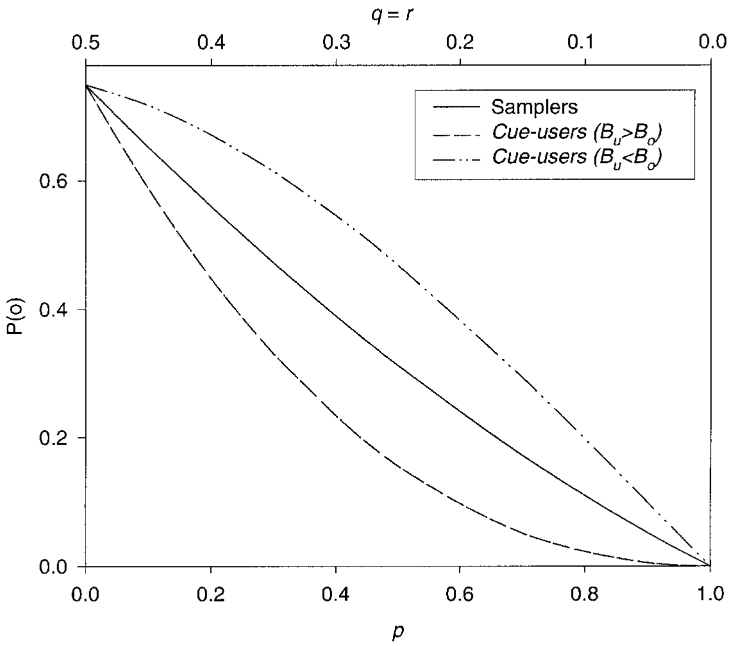

Figure 5. Probability of settling in an occupied source patch (P(o)) in relation to landscape composition for samplers and for cue-users both when $B_u < B_o$ and $B_u > B_o$. Note that only certain combinations of p, r and q are shown.

patch. So, it benefited from any increment in the ability to find the best possible patch. Cue-using strategy, conditional upon conditions, can be used both to avoid competition by and to aggregate with heterospecific individuals (see e.g., Cody, 1978; Mönkkönen et al., 1996).

Many earlier models of habitat selection have assumed that the presence of other species affects habitat selection but through an unspecified process (e.g., Rosenzweig, 1985; Morris, 1987, 1990, 1995; Brown and Pavlovic, 1992). Danielson (1991, 1992), however, explicitly assumed in his two-species model that, when species B occupies a patch, individuals of species A do not invest much time or energy in sampling that particular patch. Instead they use the resources saved to sample another patch, perhaps finding one that is unoccupied by species B. Our results show that such recognition is usually selected for.

Our model makes several assumptions about the two species. First, we assume that residents and colonists have shared habitat preferences. Previous work has focused more on species with distinct preferences (Pimm and Rosenzweig, 1981; Danielson, 1991, 1992) than with shared preferences (Rosenzweig, 1985). There is often considerable overlap in the habitat niches of different species, particularly among habitat generalists. Our model is, therefore, more likely to apply to habitat generalist (see also Mönkkönen et al., 1990, 1997; Forsman et al., 1998b). Dall and Cuthill (1997) suggested that, all else being equal, the generalist strategy is costly because generalists need to gather more information about their environment than do specialists. One way to avoid such costs would be to use information provided by other individuals.

Second, we assume that residents do not prevent colonists from settling in patches where residents have established themselves. This assumption seems realistic because interspecific territoriality is quite likely an exception in nature (Blondel 1985), observed only among congeners (Cody 1978, Robinson and Terborgh 1995). Indeed, there is evidence that territories of different species may overlap more than expected by chance alone (Reed 1982, Timonen et al. 1994).

Finally, we assumed that residents would be a reliable sign of patch quality. This assumption is robust. Residents, arriving sooner, are probably less time-constrained than colonists and, hence, can invest more time in assessing habitat quality. Thus, their distribution will be closer to ideal. Patches with high predation risk may lack residents because the latter have had time to evaluate the risk or because residents in risky patches have been consumed. Social aggregations may provide benefits not linked with the absolute quality of patches, e.g. mutual exploitation of resources leading to enhanced feeding efficiency and reduced predation rates (e.g., Alexander, 1974; Morse, 1977; Caraco and Pulliam, 1984; Latta and Wunderle, 1996).

We constructed our model to evaluate the fitness consequences for a colonizing organism from interactions with a resident species. It would be important to develop more general models which consider frequency-dependent strategy of using other individuals (both heterospecific and conspecific, and for both residents and colonists) as cues of habitat quality. Including density-dependence too, could easily make the model analytically intractable, but such models could be simulated.

Acknowledgments

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Appendix. The fitness equations derived from the choice trees in Figure 1.

For samplers (Fig. 1A):

$$\begin{aligned} W_1 = {} & p(pB_u + qB_o + rB_u - 2C_d) \\ & + q(pB_u + qB_o + rB_o - 2C_d) \\ & + r(p(pB_u + qB_o + rB_u - 3C_d) \\ & + q(pB_u + qB_o + rB_o - 3C_d) \\ & + r(B_s - 2C_d)) \end{aligned}$$

For cue-users when $B_u > B_o$ (competition, Fig. 1B):

$$\begin{aligned} W_2 = {} & p(B_u - C_d - pC_d - qC_u - rC_d) \\ & + qp(B_u - C_r - C_d - pC_d - qC_r - rC_d) \\ & + q^2(B_o - 2C_r) + qr(B_o - C_r - C_d) \\ & + r(p(B_u - 2C_d - pC_d - qC_r - rC_d) \\ & + q((q + r)(B_o - C_r - C_d) - qC_r - rC_d \\ & + p(B_u - 2C_d - C_r - pC_d - qC_r - rC_d)) + r(B_s - 2C_d)) \end{aligned}$$

For cue-users when $B_u < B_o$ (benefit, Fig 1C):

$$\begin{aligned} W_3 = {} & p((p + r)(B_u - 2C_d) + q((p + r)(B_o - 2C_d - C_r) \\ & + q(B_o - C_d - 2C_r))) + q((p + r)(B_o - C_r - C_d) \\ & + q((p + r)(B_o - C_d - 2C_r) + q(B_o - 3C_r))) \\ & + rp((p + r)(B_u - 3C_d) + q(B_o - 2C_d - C_r - (p + r)C_d - qC_r)) \\ & + rq((p + r)(B_o - 2C_d - C_r) \\ & + q(B_o - 2C_r - C_d - C_d - (p + r)C_d - qC_r)) + r^2(B_s - 2C_d) \end{aligned}$$

To solve the Conditions 1 and 2 from the expressions $W_1 < W_2$ and $W_1 < W_3$, we first collect all terms containing B_u, B_o, C_d, and C_r and get for the first inequality

$$\Phi C_d > \Phi C_r + \Psi C_r + \Psi B_o - \Psi B_u$$

and for the second

$$\Phi C_d > \Phi C_r + \Psi C_r - \Psi B_o + \Psi B_u$$

where

$$\Phi = qp + q^2p^2 - q^2 + q^3p - 2q - q^2p + q^3$$

and

$$\Psi = q^2p + p^2q - 2pq$$

It can be shown that

$$\Psi/\Phi = p/(1 + q + pq)$$

which can be used to solve the Conditions 1 and 2 (see main text).

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