

Ecological traps in changing environments: Ecological and evolutionary consequences of a behaviourally mediated Allee effect

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ABSTRACT

Species usually have to use indirect cues when assessing habitat quality. This means that it is possible for humans to alter habitats in a way that causes a discrepancy between the cues and the true quality of different habitats. This phenomenon is called an ‘ecological trap’. Here we show that the trap may lead to a behaviourally mediated Allee effect, where population growth is reduced because of non-ideal choices of individuals. The reduction is greatest at low densities because more individuals can choose their preferred habitat when competition for breeding sites is reduced. An ecological trap may lead to multiple equilibria in population dynamics and cause deterministic extinction in habitats that are capable of sustaining a viable population. We also study the efficiency of three mechanisms that may rescue a population from this extinction trap: natural selection acting on habitat preferences and two forms of phenotypic plasticity, experience-based learning and a philopatric preference for the natal habitat. Selection is most efficient in short-lived species with large heritable variation in habitat preferences, whereas in long-lived species, plastic traits outperform genetically determined preferences. The simple philopatric strategy generally produces the most favourable outcome. It hardly differs from the optimal strategy that assumes perfect and immediate knowledge of habitat change, and is very robust to non-ideal variation in the strength of habitat preferences. We conclude that conservation biologists need to ensure that cues for habitat choice correlate with habitat quality.

Keywords: ecological trap, extinction, habitat selection, ideal despotic distribution, philopatry, social learning, source–sink dynamics.

INTRODUCTION

The Allee effect is defined as a decrease in individual survival or breeding output at low population sizes. It is critical to many issues in population ecology (Dennis, 1989), including extinctions (Reed, 1999; Berec *et al.*, 2001), exploitation (Greene *et al.*, 1998; Petersen and Levitan, *in press*), social behaviour (Courchamp *et al.*, 1999; Stephens and Sutherland,

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1999) and the limits of species' ranges (Stephens and Sutherland, 1999; Keitt *et al.*, 2001). There is widespread evidence for the Allee effect in mammals (e.g. Komers and Curman, 2000), birds (e.g. Green, 1997) and fish (e.g. Liermann and Hilborn, 1997). Two recent reviews (Courchamp *et al.*, 1999; Stephens and Sutherland, 2000) present several alternative ways in which Allee effects may originate. These include dilution of predation risk at increasing group sizes (Hamilton, 1971; Treherne and Foster, 1982), increased predation at low population densities that follows reduced vigilance (Kenward, 1978; Berg *et al.*, 1992), interspecific kleptoparasitism (Carbone *et al.*, 1997), difficulties in finding a mate (Kuussaari *et al.*, 1998; Berec *et al.*, 2001) and distorted sex ratios (Soldaat *et al.*, 1997). Stephens *et al.* (1999) point out that the Allee effect is often defined in one of two ways. The component Allee effect, typically addressed in empirical studies, applies when a factor that decreases the performance of the population, such as predation or lack of fertilization, is shown to be most severe at low densities. It does not necessarily follow, however, that total fitness declines (Stephens *et al.*, 1999). In the demographic Allee effect, which is usually used by theoreticians, total fitness declines at low density. This latter effect is directly linked to population regulation and it is the focus of this study.

Here, we show how a novel type of an Allee effect can be produced by maladaptive habitat choice that leads to an 'ecological trap'. An ecological trap occurs when environmental change decouples the cues that individuals use to assess habitat quality from the true quality of the environment (Dwernychuk and Boag, 1972; Gates and Gysel, 1978). Such change is often associated with human activity, such as introducing new competitors or predators to an area, or changes in agricultural practices or other types of land use (Best, 1986). If, as a result, the environmental cues that individuals of a given species use for habitat quality become outdated, previously optimal rules of habitat selection may lead to a reduction in fitness and population-level breeding performance. Since more individuals can use their preferred habitat when there are few competitors, this reduction is especially pronounced at low densities – which corresponds to the definition of the Allee effect.

How common are ecological traps and Allee effects? A common objective in the study of habitat selection has been to derive population processes from the behaviour of individuals, and such models typically produce negative (i.e. direct) density dependence without any Allee effects. For example, negative density dependence can be predicted from applying ideal free models to foraging decisions (Goss-Custard *et al.*, 1995a,b) or ideal despotic models to territory choice (Sutherland, 1996; Kokko and Sutherland, 1998). An assumption of these models is that individuals are ideal: they settle where their fitness will be greatest. There are indeed many examples of this in which the preferred habitat is of better quality, measured by intake rate (Zwarts, 1976), survival rate (Morris, 1996) or breeding success (Dhondt *et al.*, 1992; Ferrer and Donazar, 1996; Martin, 1998), and as the population size increases an increasing proportion move into the poorer habitat. In reality, sampling errors will often cause a discrepancy between the ideal and the observed distribution (Abrahams, 1986), but this has usually been considered as perceptual constraints resulting in noise around the optimal decision. Alternatively, judgement of habitat qualities may suffer from systematic biases, which is the focus of this paper. We refer to these as perceptual errors.

Perceptual errors presumably occur because of the difficulty in distinguishing between sites of different qualities. This is a particular problem when the information is inevitably incomplete, for example because territories are selected before it is possible to assess prey

abundance (Orians and Wittenberger, 1991), or because much of the variation in quality is due to predators, parasites, risk of physical events such as flooding, human disturbance or disruptive agricultural activities that are all difficult to assess during settlement. Animals often have to use cues rather than assess actual measures of mean reproductive output. This may lead to gross errors, such as mayflies laying eggs on asphalt roads as they reflect strongly horizontally polarized light, like light reflected from a water surface of a pond (Kriska *et al.*, 1998), or diving beetles (*Dytiscus marginalis*) landing in beer (W.J. Sutherland, personal observation).

As further examples of perceptual errors, Kentish plovers (*Charadrius alexandrinus*) have been shown to prefer nesting in a site with an abundant food supply although it also has high densities of predators, so that those nesting in the less preferred areas have higher breeding success (Székely, 1992). Lapwings (*Vanellus vanellus*) select lush green fields, but in intensive farming landscapes these are often highly fertilized cereal fields, and the birds usually abandon their nests as the cereals grow rapidly (Galbraith, 1989). Morton (1987) attempted to re-establish song wrens (*Cyphorhinus phaeocephalus*) onto Barro Colorado Island, Panama. Wrens often nested along trails that appeared like their natural stream habitat, but had a high predation rate, presumably because many predators used the trails. Barnacle geese (*Branta leucopsis*) on their spring staging grounds prefer coastal saltmarsh to agricultural fields, although feeding in the latter results in higher weight gain and the individuals returning in the autumn with more young (Black *et al.*, 1991). In Baltic populations of the barnacle goose, reproductive success declines rapidly as colonies grow, yet females remain philopatric regardless of colony size (Van der Jeugd, 1999). Skylarks (*Alda arvensis*) select silage fields to nest in even though nests practically never succeed (P. Lynas and W.I. Montgomery, personal communication). Sage sparrows (*Amphispiza belli*) in southern California were shown to have a preference for habitat types that resulted in lower reproductive success (Misenhelter and Rotenberry, 2000), which the study's authors speculated was a consequence of anthropogenic habitat change influencing the distribution of predatory snakes. California towhees (*Pipilo crissalis*) select dense ungrazed oak-pine woodlands, although more open grazed areas have a higher reproductive success as a result of lower predation (Purcell and Verner, 1998). Oystercatchers (*Haematopus ostralegus*) were found to have only nested alongside rivers in northern England once the coastal sites were full, even though the breeding success was markedly higher inland (K. Briggs, personal communication). Furthermore, coastal birds only nested on nearby slag heaps when the other (less successful) sites were occupied (K. Briggs, personal communication). Such discrepancies between cues and quality are likely to be of increasing importance as the landscape becomes increasingly modified due to human activities.

In addition to investigating the threat to populations caused by ecological traps, we study the efficiency of three processes in rescuing a population from the trap. The first process is natural selection acting on habitat preferences in the new environment (Partridge, 1978; Jaenike and Holt, 1991). The second and third options are two forms of phenotypic plasticity: learned habitat preferences (from individual experience: Baeyens, 1981; Beletsky and Orians, 1987; Petersen and Best, 1987; Haas, 1998; Schjørring *et al.*, 2000; or from watching others: Boulinier and Danchin, 1997; Schjørring *et al.*, 1999) and philopatric preferences (McPeck and Holt, 1992). We show that any of these processes may rescue a population from the trap, but their efficiency varies according to the life history of the species concerned.

MAL-ASSESSMENT IN CHANGING HABITATS

For simplicity, we consider two suitable habitats, A and B, filled in an ideal despotic manner. To provide an illustrative example, we assume that habitat quality only affects the probability that a brood of N offspring fledge successfully (hereafter termed productivity), but not the brood size or the subsequent survival of offspring or parents. Habitat A is overall of higher quality than B, so that the best breeding site in habitat A has the highest productivity of all territories. In both A and B, however, productivity varies spatially, so that the worst territories in A may produce fewer offspring than the best ones in habitat B. Therefore, after a certain fraction of habitat A is filled by territories, it becomes beneficial for additional individuals to use either habitat B or A, by choosing the highest productivity among the vacant territories. This produces the ideal despotic distribution (Fretwell and Lucas, 1970). Density dependence is generated through declining average breeding success, as worse territories have to be used for breeding with increasing population size (Rodenhouse *et al.*, 1997).

If the productivity of habitat A is reduced, a population decline follows. However, the magnitude of the decline depends on whether or not individuals adjust their habitat preferences to the change in habitat qualities. To study the extremes of possibilities, we first investigate the changes in density dependence and equilibrium population sizes in two cases: (1) individuals instantly switch to follow the new ideal despotic distribution (i.e. they have immediate complete knowledge of the new productivity of A compared to B) and (2) individuals perceive no change in their fitness in habitat A.

In the latter case, a possibility of a behavioural Allee effect emerges: the population will grow poorly at low population densities, since most individuals will use the preferred but poor habitat A (Fig. 1a). As the population grows to reach higher densities, however, it will start to perform almost as well as in the case with new ideal behaviour, since enough individuals are 'forced' to use the now better habitat B. Thus, the reduction in equilibrium densities caused by suboptimal behaviour may be negligible (Fig. 1a).

With larger reductions in habitat quality, three equilibria emerge if individuals have no knowledge of the change. In addition to the equilibrium with a reduction almost as small as the new ideal distribution would allow, there exists an alternative with a very much larger reduction in population size, and an unstable equilibrium between these two that determines which of the stable equilibria will be approached (Fig. 1b). Thus, if the population size is large, there are sufficient individuals breeding in the now better habitat B to keep average productivity high. At low sizes, however, only habitat A will be used, resulting in insufficient growth to reach the more favourable equilibrium. Given that the initial population size is high before the quality reduction, the larger equilibrium is initially the more likely one. However, stochastic fluctuations may well bring the population down to the low equilibrium, which is especially likely to happen if environmental fluctuations or random catastrophes occasionally bring populations below equilibrium levels (see below).

If the quality of habitat A is further reduced (Fig. 1c,d), one or both of the stable equilibria may disappear. Population extinction because of old behavioural preferences is thus possible, even though the less preferred but still intact habitat B alone could support a reasonably large population. In the example of Fig. 1c,d, more than 50% of the previous population size could be maintained, assuming a transition to preferring habitat B; yet extinction is certain in Fig. 1d, assuming no change in individual behaviour.

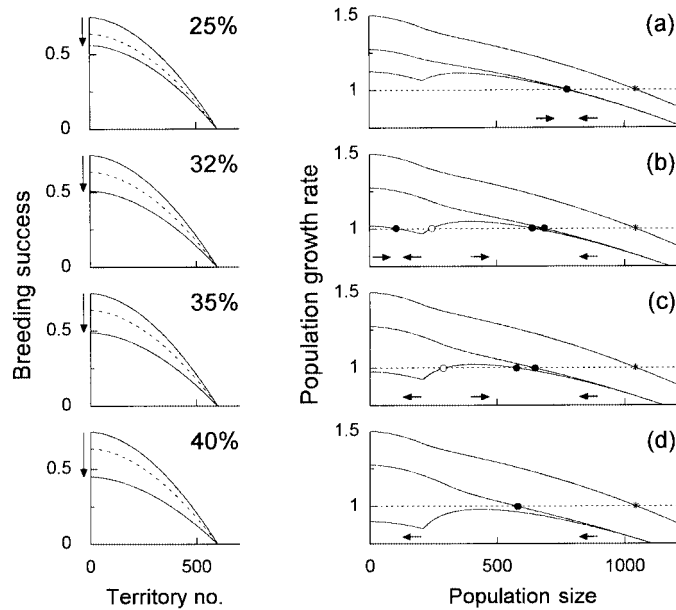


Fig. 1. The ideal despotic distribution with deteriorating habitat quality in the better habitat. Left-hand panels show declining productivity (measured as proportion of successful breeding attempts) of territories in habitat A (solid lines) and B (dashed line) when additional lower-quality territories are used. The two lines of A indicate its initial productivity as well as the lowered productivity due to habitat change (marked with arrow), and the number indicates a , the magnitude of habitat deterioration. Panels on the right-hand side show per capita rates of population increase for the undisturbed environment (uppermost line, equilibrium density marked with a star), the disturbed environment where individuals have complete knowledge of the change, and the disturbed environment where individuals distribute themselves according to the old quality difference between A and B (lowest line). Open and filled dots indicate stable and unstable equilibria, respectively, and arrows indicate the direction of population change in the case of old knowledge. As the deterioration of habitat A increases from (a) to (d), the Allee effect generated by sub-optimal behaviour becomes stronger and may lead to population extinction from any initial population size, even though the environment as such were still capable of sustaining a viable population (case (d)).

The Allee effect, as generated in the above examples (Fig. 1), does not rely on the assumption that the qualities of breeding sites decline according to the same relationship in habitats A and B, thus requiring individuals to compare the relative qualities of available territories in A or B. Similar decreases in population growth are always expected when previously superior sites become inferior to less preferred ones; for example, in a case where territories in habitat A were originally always more productive than those in habitat B (Fig. 2). Continuing unconditional preference for habitat A will result in a behaviourally mediated Allee effect, if the quality of A deteriorates sufficiently (Fig. 2).

ADAPTING TO THE CHANGE: NATURAL SELECTION VERSUS INDIVIDUAL PLASTICITY

Clearly, it would be beneficial for individuals to ‘learn’ about the change in habitat qualities. Apart from being evolutionarily suboptimal, a failure to do so may also result in population extinction (Fig. 1d), even if the remaining habitat could support a viable population. There are two possible ways of ‘learning’ the new habitat ranking, either by natural selection or by pre-existing plasticity at the individual level. The former assumes heritable variation in habitat preferences. The latter utilizes responses to experiences during an individual’s lifetime and we investigate two possible forms of plasticity. First, individuals may learn to prefer habitats where their own breeding attempts have been successful. We investigate the simplest possible form of such a learning rule, where individuals switch their preference to the alternative habitat type if their breeding attempt failed in the currently used habitat, but ignore any earlier experiences. Secondly, individuals may simply prefer the habitat type in which they were born (a form of philopatry extended to cover the whole habitat type, not just the natal territory).

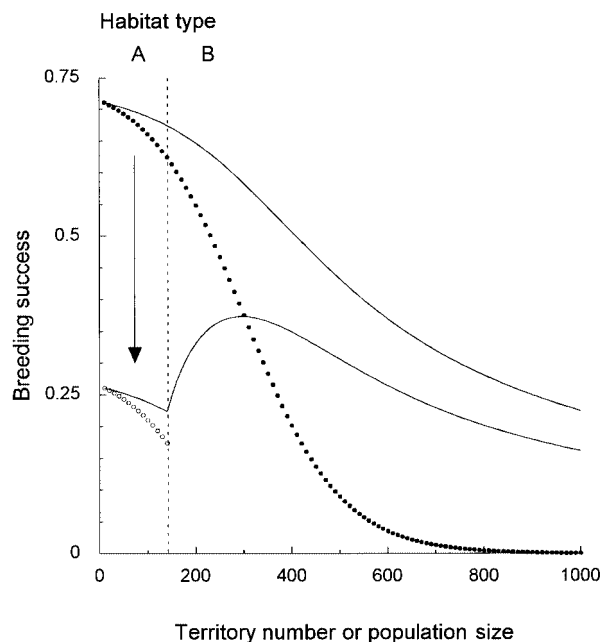


Fig. 2. The behavioural Allee effect in an environment with 1000 potential breeding sites, of which the best 140 are of the superior habitat type A and the rest are of type B. Solid dots give expected breeding success in these sites, indicating that the worst territory in habitat A is superior to the best in habitat B. The upper solid line gives the average breeding success in a population of given size, assuming an ideal despotic distribution; at population size n , this is an average of the success in territories 1 to n . If the quality of habitat A deteriorates (arrow), leading to breeding success in A described by the open dots, the old habitat choice rule will lead to much reduced average breeding success at low densities (lower solid line).

Simulating responses to habitat change

We simulated the response of two populations, one with a ‘fast’ (annual adult survival $S = 0.5$, brood size $N = 4$) and one with a ‘slow’ life history (annual adult survival $S = 0.8$, brood size $N = 1$), to a reduction in the quality of habitat A as defined in Fig. 1. We additionally assume that juvenile first-winter survival is half of that of adults. Both life histories lead to the same lifetime reproductive success in a habitat with equal productivity, f (since $4 \times 0.25/(1 - 0.5) \times f = 1 \times 0.4/(1 - 0.8) \times f$), and thus both can be made to obey the same shape of density dependence.

Density dependence is generated as in Fig. 1, so that lower-quality territories have a smaller chance of fledging a brood of offspring. In our example, the productivity (probability that a brood fledges) of the n th territory in habitat A is given by $f_A(n) = 0.75(1 - (0.00167n)^{1.8})$ and is initially 15% lower in habitat B. The strength of preference for habitat A is measured by P_i , which may vary among individuals; it is an individual’s estimate of the overall quality difference $f_A(n)/f_B(n)$ between habitats (which is constant for different values of n). If $P_i < 1$, the individual prefers habitat B over A. However, individuals also take relative site quality into account. An individual will thus settle in the n_A th site in habitat A rather than in the n_B th of habitat B, if $P_i f(n_A) > f(n_B)$. If P_i estimates $f_A(n)/f_B(n)$ correctly, this will result in ideal behaviour (the ideal despotic distribution).

The simulation starts at the equilibrium population size for the non-deteriorated habitat. At the start of the simulation, the productivity of all territories in habitat A deteriorates by a fraction a . Throughout the simulation, the preference values P_i will be attributed to individuals according to the following alternative rules:

1. *Old preferences*: P_i ’s are fixed to the value $f_A(n)/f_B(n)$ that was optimal (produced the ideal despotic distribution) before the habitat change, i.e. individuals have no knowledge of the change in habitat qualities.
2. *Optimal preferences*: P_i ’s are fixed to the optimal value $(1 - a) f_A(n)/f_B(n)$ immediately after the habitat change, which produces the ideal despotic distribution in the new circumstances.
3. *Genetically inherited preferences*: initial P_i ’s are normally distributed with mean $f_A(n)/f_B(n)$ (the old ideal preference) and variance σ^2 , and offspring inherit the preference of their parent. For simplicity, we assume haploid inheritance.
4. *Learned preferences*: offspring initially have no knowledge of the habitat change ($P_i = f_A(n)/f_B(n)$), but an individual who has bred successfully will switch to a preference for the current breeding habitat ($P_i = P_C$ if breeding in habitat A, or $P_i = 1/P_C$ if breeding in habitat B). If the current attempt failed, it will prefer the other habitat in the next breeding attempt ($P_i = 1/P_C$ if breeding in habitat A, or $P_i = P_C$ if breeding in habitat B). We consider two values of P_C , 1.2 and 2.0. The former yields roughly correct estimates of habitat quality differences if the correct habitat is preferred (both initially, when $P_C = 1.2$ corresponds to $f_A(n)/f_B(n) = 1.18$; and after habitat change, when $1/P_C = 0.83$ falls within the range of $(1 - a)f_A(n)/f_B(n)$ studied here). The latter value, $P_C = 2.0$, clearly overestimates habitat quality differences. It is included to investigate robustness of plastic behaviour, when the true difference in habitat qualities is unknown to individuals.
5. *Philopatric preferences*: offspring born in habitat A obtain a constant preference of magnitude P_C ($P_i = P_C > 1$) for that habitat. Offspring born in habitat B prefer habitat B equally strongly, $P_i = 1/P_C$. Values of P_C are either 1.2 or 2.0, as above.

After breeding, each parent survives with probability S (0.5 or 0.8 depending on the life history) and each offspring survives with probability $S/2$ (0.25 or 0.4). We also include the possibility of random catastrophes, in which case a catastrophe occurs in each year with probability $C = 0.03$. Survival of both parents and offspring is halved in a catastrophic year. If catastrophes do not occur, demographic stochasticity is the only source of variation, affecting breeding success and survival, as outlined above. Surviving individuals choose new territories in random order. Each individual in turn compares the best available territory in habitat A to the best territory in habitat B, and makes the choice according to its preference value P_i . One hundred realizations of simulations were run for 200 breeding seasons for each value of a , yielding final population sizes for each of the preference options.

Simulation results

Examples of the simulation output (Fig. 3) show transitions between equilibria in three different populations: one that behaves as if A were still the better habitat (old preferences, Fig. 3a), one that has perfect knowledge of the change (optimal preferences, Fig. 3b) and one that evolves according to inherited habitat preferences (genetically inherited preferences, Fig. 3c), with initial variation in preferences $\sigma = 0.1$. For purposes of comparison, each population is subjected to catastrophes four times in 200 years: at times 20, 50, 160 and 180. At the start of the simulation, habitat A deteriorates by 32% ($a = 0.32$), which in the deterministic model produces three equilibria (Fig. 1c).

Each of these three populations shows an initial decline from the original equilibrium of 1000 individuals (Fig. 3), which is to be expected because of lowered productivity in habitat A (Fig. 1). The responses to catastrophes are different, however. In the population of Fig. 3a, the first catastrophe is followed by a recovery, but there is a decline rather than a recovery after the second catastrophe. The population now fluctuates around a much lower equilibrium (cf. Fig. 1c), caused by the small population no longer utilizing the growth possibilities in habitat B as every breeder can find a territory in the preferred but low-quality habitat A. At this equilibrium, individual numbers are low such that two later catastrophes, together with demographic stochasticity, are sufficient to cause extinction (Fig. 3a). If the population, however, immediately 'knows' to use preferentially habitat B, it will recover from repeated catastrophes (Fig. 3b). Finally, a population where most individuals initially prefer habitat A may survive by evolving a preference for B (Fig. 3c). However, in this case, the proportion of individuals using habitat B is still low after the first catastrophe (year 20), and it is conceivable that this could have led to extinction had there been slightly less genetic variation or if catastrophes had been more frequent.

In general, population sizes will fall when the productivity of the preferred habitat falls, but the magnitude of the decline depends strongly on the habitat choice rules of the population (Fig. 4). Optimal preferences will produce the highest population sizes (median between 400 and 600 individuals), with no simulated populations going extinct even in the presence of random catastrophes (Fig. 4). By contrast, the extinction probability of populations using the old habitat preferences can be very high under the same circumstances. Under both 'slow' and 'fast' life histories, a 35% reduction in habitat quality, together with a relatively low frequency of catastrophic years (3%), leads to an extinction risk exceeding 50%, and only 10% of cases still maintain population sizes above 100 individuals after 200 years (Fig. 4a,b). This shows that the danger outlined in Fig. 3a is not an exceptional outcome. A slightly more severe habitat quality reduction (40%,

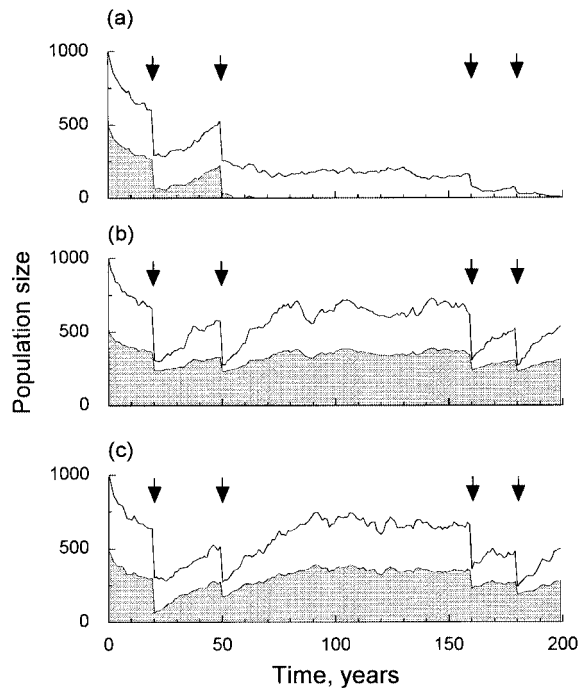


Fig. 3. Simulation of a population with a 'fast' life history using (a) old preferences, (b) optimal preferences and (c) genetically inherited preferences in habitat choice. See text for details of the simulation and density dependence. For illustrative purposes, catastrophes are in this example fixed to occur at times $t = 20, 50, 160$ and 180 years (marked with arrows). The quality of habitat A deteriorates at time $t = 0$ (start of the simulation) by 32%, resulting in a population decline from the initial equilibrium of 1000 individuals. The shaded area indicates numbers of individuals breeding in habitat B, while the white area gives numbers in the (formerly better and now worse) habitat A. Thus, the upper line gives total population size. In (a), the population does not recover from repeated catastrophes, as no breeding occurs in habitat B at small population sizes. In (b), the population always maintains a large fraction of individuals breeding in habitat B, and the population is able to recover from catastrophes. In (c), the first catastrophe almost eradicates the population breeding in habitat B. Selection, however, increases the proportion of individuals favouring B fast enough so that, by the time of the second catastrophe, the population response resembles the case of optimal preferences (b) more than that of old preferences (a).

cf. Fig. 1d) predicts extinction due to the behaviourally generated Allee effect; here, the simulated extinction probability reaches 90% in 200 years in populations using old behavioural rules, whereas new rules again save all populations from extinction (Fig. 4c,d). In simulated populations that are not subject to random catastrophes, the time to extinction is clearly longer. Population size distributions therefore shift to the right, but the relative order of new and old habitat choice rules still applies: new rules always produce higher population sizes than old ones (not shown).

Clearly, a transition from the old habitat choice rules to a rule that at least resembles the new ideal despotic distribution is needed to avoid the behavioural Allee trap. All of the

three alternatives studied – natural selection on genetically determined habitat preferences, philopatric plasticity and learning – can rescue the population from the Allee effect, but with highly varying efficiency, which also depends on the type of life history (Fig. 4). Natural selection produces population distributions that deviate only little from the new ideal despotic distribution, provided that there is pronounced genetic variation in habitat preferences ($\sigma = 0.1$ in the examples of Fig. 4). However, evolution may not produce types with better habitat preferences fast enough to avoid extinction, if genetic variability is smaller ($\sigma = 0.05$ in Fig. 4). This leads to a dichotomous distribution of population sizes 200 years after the habitat change; for example, in Fig. 4b, some 10% of the runs with $\sigma = 0.05$ end up with relatively high population sizes where new genotypes have taken over, but in the remaining cases the population follows the fate of the old preferences for long enough to become extinct or trapped at very low densities. This phenomenon is similar

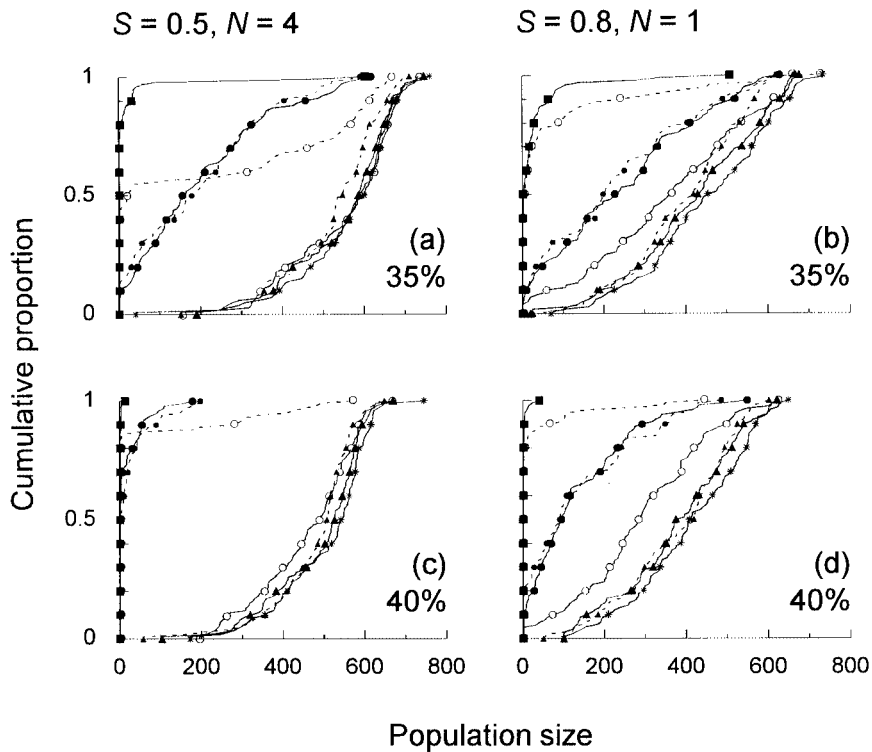


Fig. 4. Population size distributions after 200 years of simulation, when the quality of the preferred habitat is reduced by a fraction α (given as a percentage) at time $t = 0$. The cumulative plot indicates high population sizes when the graph is far to the right, and extinction is indicated by the graph hitting the y-axis. Behavioural rules used: squares: old preferences; stars: optimal (new) preferences; open dots with solid line: natural selection (genetically inherited preferences), $\sigma = 0.1$; open dots with dashed line: natural selection (genetically inherited preferences), $\sigma = 0.05$; large filled dots with solid line: learned preferences, $P_C = 1.2$; small filled dots with dashed line: learned preferences, $P_C = 2.0$; large triangles with solid line: philopatric preferences, $P_C = 1.2$; small triangles with dashed line: philopatric preferences, $P_C = 2.0$.

to the situation envisaged by Dolman and Sutherland (1995), in which survival of the population depends on finding a new migratory route, and populations may decline to very low densities before the alternative allele takes over. We also find that natural selection always works more efficiently, producing higher population sizes and fewer extinctions, under a 'fast' than a 'slow' life history (Fig. 4). Clearly, natural selection may require large amounts of genetic variation to be sufficiently efficient in shaping habitat preferences in a changing world, especially in species with long generation times.

Plastic preferences, on the other hand, prove more efficient in long-lived species. Plastic learning does not avoid extinctions or allow the population to maintain high densities as efficiently as perfect knowledge of the new ideal despotic distribution, but in terms of population persistence it clearly outperforms natural selection when there is little genetic variation in habitat preferences (Fig. 4). On the other hand, in cases where natural selection is efficient (i.e. when there is large genetic variation in habitat preferences), selection may make populations perform better than under learning. By contrast, the strength of the learned preference ($P_C = 1.2$ or 2.0) is relatively unimportant for population persistence or size (Fig. 4).

Surprisingly, the very simple rule of philopatric preferences performs extremely well (Fig. 4). When the preference is not very strong ($P_C = 1.2$), it produces population size distributions hardly distinguishable from the new ideal despotic distribution. Even with large overestimates of the ratio of habitat qualities ($P_C = 2.0$), philopatric preferences still always prevent extinction and never deviate from the ideal population size by more than 100 individuals.

DISCUSSION

Cues used for habitat choice are often indirect, as individuals cannot predict breeding success directly but have to rely on proxies of fitness in different habitats. This means that there is a possibility that humans may change the quality of the environment without changing the cue; for example, by introducing a predator that inhabits a specific habitat but does not change the appearance of the habitat from the native species' viewpoint. We have shown that if individuals continue to prefer the habitats according to the old cues, they will distribute themselves at different population sizes in a way that reduces population growth rates at low densities – a behaviourally mediated Allee effect. If strong enough, this process may lead to deterministic population extinction in an environment that, as such, has a positive carrying capacity and would be able to maintain a viable population.

Population persistence in changing environments may, therefore, require changing habitat preferences. One possible agent, natural selection acting on innate habitat preferences, often produces a dichotomous distribution of population sizes, where populations perform very well if they survive an initial bottleneck, but may also go extinct during this process. The efficiency of natural selection in avoiding the 'extinction trap' depends both on the amount of genetic variation present and on the life history of the species: those with short generation times and high genetic variation should adapt quickest to the new situation, whereas 'slow' species may go extinct before they have had time to adapt to the new circumstances. 'Slow' species survive best in new conditions if individuals rely on plastic habitat choice rules, whereas 'fast' species may perform better if their preferences are genetically determined.

Opportunities for learning are limited in short-lived species, since learning only improves the behaviour of older individuals and this may be insufficient to maintain the population. For example, in a species where adult survival equals 0.5, the average breeder has two breeding attempts throughout its lifetime. Fifty per cent of breeding birds will therefore always be naive and bound to make incorrect choices. With 80% adult survival, the proportion of naive birds drops to 20%, which explains why plastic learning produces higher population sizes in long-lived species.

The very simple rule of philopatric habitat preferences performs surprisingly well, always equalling or clearly exceeding the result from natural selection, and producing population sizes that differ only slightly from the distribution that completely optimal choices would generate. The logic behind this result is simple: the fact of being born provides an individual with information that it has, with a high likelihood, originated from a high-quality patch (Pärt, 1991). Selection for philopatry will occur when habitat quality has fluctuated in a manner that individuals have difficulty detecting. The evolutionary advantage of philopatry may be considerable; a recent modelling study has shown that the fitness difference between a simple philopatric strategy and a strategy with complete knowledge may be negligible (J.M. McNamara, I.C. Cuthill and S. Dall, unpublished manuscript).

Both examples of plastic behaviour, philopatry and learning, are also surprisingly good in the sense that they are very robust to changes in the strength of the preference. In our simulations, populations grew or survived almost equally well with preferences that clearly overestimate the difference in habitat qualities as with preferences which are more finely tuned – the mechanism that generates the preferences in individuals is far more important than the strength of preferences as such.

Our comparison between the genetic preferences and the two alternatives of plastic behaviour does not consider evolutionary optimality: optimal behaviour in all cases would be to choose habitats according to the ideal despotic distribution (hence the comparison to ‘optimal preferences’). Any strategy with non-ideal behaviour is less profitable for the individual than ideal behaviour, in addition to threatening the population. We have considered non-ideal responses for the simple reason that they are likely to exist: there is no reason why a population experiencing a sudden change in habitat qualities would gain immediate and complete knowledge of the new relationship between environmental cues and habitat qualities.

We have shown that a preference for a sink habitat can result in population extinction in areas that would otherwise be capable of sustaining a population. As a corollary, adding new habitat that appears to be of high quality, but is not, may increase the likelihood of extinction. Species relying on genetically inherited habitat preferences appear most vulnerable to such changes, whereas populations where learning and cultural transmission are in use are more robust, even though they rarely reach the highest possible population sizes. Apart from the interest for evolutionary and population ecology, this has clear conservation implications as well. First, conservationists need to pay attention to the habitat choice rules used in a population, and recognize cases where a mismatch between preferences and habitat qualities could lead to sudden reductions in population sizes. Second, when managing habitats, it is necessary to consider not just the actual habitat quality, but also the perceived quality. Creating high-quality habitat without the right cues will be of little use, while allowing poor-quality habitat to appear very suitable might be damaging to the entire population.

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REFERENCES

- Abrahams, M.V. 1986. Patch choice under perceptual constraints: A cause for deviations from an ideal free distribution. *Behav. Ecol. Sociobiol.*, **19**: 409–415.
- Baeyens, G. 1981. Functional aspects of serial monogamy: The magpie pair bond in relation to its territorial system. *Ardea*, **69**: 145–166.
- Beletsky, L.D. and Orians, G.H. 1987. Territoriality among male red-winged blackbirds. 2. Removal experiments and site dominance. *Behav. Ecol. Sociobiol.*, **20**: 339–349.
- Berec, L., Boukal, D.S. and Berec, M. 2001. Linking the Allee effect, sexual reproduction, and temperature-dependent sex determination via spatial dynamics. *Am. Nat.*, **157**: 217–230.
- Berg, A., Lindberg, T. and Källebrink, K.G. 1992. Hatching success of lapwings on farmland: Differences between habitats and colonies of different sizes. *J. Anim. Ecol.*, **61**: 469–476.
- Best, L.B. 1986. Conservation tillage: Ecological traps for nesting birds? *Wildlife Soc. Bull.*, **14**: 308–317.
- Black, J.M., Deerenberg, C. and Owen, M. 1991. Foraging behaviour and site selection of barnacle geese *Branta leucopsis* in a traditional and newly colonised spring staging habitat. *Ardea*, **79**: 349–358.
- Boulinier, T. and Danchin, E. 1997. The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. *Evol. Ecol.*, **11**: 505–517.
- Carbone, C., DuToit, J.T. and Gordon, I.J. 1997. Feeding success in African wild dogs: Does kleptoparasitism by spotted hyenas influence hunting group size? *J. Anim. Ecol.*, **66**: 318–326.
- Courchamp, F., Grenfell, B. and Clutton-Brock, T. 1999. Inverse density dependence and the Allee effect. *Trends Ecol. Evol.*, **14**: 405–410.
- Dennis, B. 1989. Allee effects: Population growth, critical density, and the chance of extinction. *Nat. Res. Model.*, **3**: 481–538.
- Dhondt, A.A., Kempenaers, B. and Adriaensens, F. 1992. Density-dependent clutch size caused by habitat heterogeneity. *J. Anim. Ecol.*, **61**: 643–648.
- Dolman, P.M. and Sutherland, W.J. 1995. The response of bird populations to habitat loss. *Ibis*, **137**: S38–S46.
- Dwernychuk, L.W. and Boag, D.A. 1972. Ducks nesting in association with gulls – an ecological trap? *Can. J. Zool.*, **50**: 559–563.
- Ferrer, M. and Donazar, J.A. 1996. Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish Imperial Eagles. *Ecology*, **77**: 69–74.
- Fretwell, S.D. and Lucas, J.H.J. 1970. On territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheor.*, **19**: 16–36.
- Galbraith, H. 1989. Arrival and habitat use by lapwings *Vanellus vanellus* in the early breeding season. *Ibis*, **131**: 377–388.
- Gates, J.E. and Gysel, L.W. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology*, **59**: 871–883.
- Goss-Custard, J.D., Caldow, R.G., Clarke, R.T., Durell, S.E.A.L.D. and Sutherland, W.J. 1995a. Deriving population parameters from individual variations in foraging behaviour. I. Empirical game theory distribution model of oystercatchers *Haematopus ostralegus* feeding on mussels *Mytilus edulis*. *J. Anim. Ecol.*, **64**: 265–276.
- Goss-Custard, J.D., Caldow, R.G., Clarke, R.T. and West, A.D. 1995b. Deriving population

- parameters from individual variations in foraging behaviour. II. Model tests and population parameters. *J. Anim. Ecol.*, **64**: 277–289.
- Green, R.E. 1997. The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. *J. Anim. Ecol.*, **66**: 25–35.
- Greene, C., Umbanhowar, J., Mangel, M. and Caro, T. 1998. Animal breeding systems, hunter selectivity and consumptive use in wildlife conservation. In *Behavioral Ecology and Conservation Biology* (T.M. Caro, ed.), pp. 271–305. Oxford: Oxford University Press.
- Haas, C.A. 1998. Effects of prior nesting success on site fidelity and breeding dispersal: An experimental approach. *Auk*, **115**: 929–936.
- Hamilton, W.D. 1971. Geometry for the selfish herd. *J. Theor. Biol.*, **31**: 295–311.
- Jaenike, J. and Holt, R.D. 1991. Genetic variation for habitat preference – evidence and explanations. *Am. Nat.*, **137**: S67–S90.
- Keitt, T.H., Lewis, M.A. and Holt, R.D. 2001. Allee effects, invasion pinning, and species' borders. *Am. Nat.*, **157**: 203–216.
- Kenward, R.E. 1978. Hawks and doves: Factors affecting success and selection in goshawk attacks on woodpigeons. *J. Anim. Ecol.*, **47**: 449–460.
- Kokko, H. and Sutherland, W.J. 1998. Optimal floating and queuing strategies: Consequences for density dependence and habitat loss. *Am. Nat.*, **152**: 354–366.
- Komers, P.E. and Curman, G.P. 2000. The effect of demographic characteristics on the success of ungulate re-introduction. *Biol. Conserv.*, **93**: 187–194.
- Kriska, G., Horvath, G. and Andrikovics, S. 1998. Why do mayflies lay their eggs en masse on dry asphalt roads? Water-imitating polarized light reflected from asphalt attracts *Ephemeroptera*. *J. Exp. Biol.*, **201**: 2273–2286.
- Kuussaari, M., Saccheri, I., Camara, M. and Hanski, I. 1998. Allee effect and population dynamics in the Glanville fritillary butterfly. *Oikos*, **82**: 384–392.
- Liermann, K. and Hilborn, R. 1997. Depensation in fish stocks: A hierarchic Bayesian meta-analysis. *Can. J. Fish. Aquat. Sci.*, **54**: 1976–1984.
- Martin, T.E. 1998. Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology*, **79**: 656–670.
- McPeck, M.A. and Holt, R.D. 1992. The evolution of dispersal in spatially and temporally varying environments. *Am. Nat.*, **140**: 1010–1027.
- Misenhelter, M.D. and Rotenberry, J.T. 2000. Choices and consequences of habitat occupancy and nest site selection in sage sparrows. *Ecology*, **81**: 2892–2901.
- Morris, D.W. 1996. Temporal and spatial population dynamics among patches connected by habitat selection. *Oikos*, **75**: 207–219.
- Morton, E.S. 1987. Reintroduction as a method of studying bird behaviour and ecology. In *Restoration Ecology* (W.R. Jordan, III, M.E. Gilpin and J.D. Aber, eds), pp. 165–172. Cambridge: Cambridge University Press.
- Orians, G.H. and Wittenberger, J.F. 1991. Spatial and temporal scales in habitat selection. *Am. Nat.*, **137**: S29–S49.
- Pärt, T. 1991. Philopatry pays: A comparison between collared flycatcher sisters. *Am. Nat.*, **138**: 790–796.
- Partridge, L. 1978. Habitat selection. In *Behavioural Ecology: An Evolutionary Approach* (J.R. Krebs and N.B. Davies, eds), pp. 351–376. Oxford: Blackwell.
- Petersen, K.L. and Best, L.B. 1987. Territory dynamics in a sage sparrow population: Are shifts in site use adaptive? *Behav. Ecol. Sociobiol.*, **21**: 351–358.
- Petersen, C.W. and Levitan, D.R. in press. The Allee effect: A barrier to recovery by exploited species. In *Conservation of Exploited Species* (J.D. Reynolds, G.M. Mace, K.H. Redford and J.G. Robinson, eds). Cambridge: Cambridge University Press.
- Purcell, K.L. and Verner, J. 1998. Density and reproductive success of California Towhees. *Conserv. Biol.*, **12**: 442–450.

- Reed, J. M. 1999. The role of behavior in recent avian extinctions and endangerments. *Conserv. Biol.*, **13**: 232–244.
- Rodenhouse, N.L., Sherry, T.W. and Holmes, R.T. 1997. Site-dependent regulation of population size: A new synthesis. *Ecology*, **78**: 2025–2042.
- Schjørring, S., Gregersen, J. and Bregnballe, T. 1999. Prospecting enhances breeding success of first-time breeders in the great cormorant, *Phalacrocorax carbo sinensis*. *Anim. Behav.*, **57**: 647–655.
- Schjørring, S., Gregersen, J. and Bregnballe, T. 2000. Sex difference in criteria determining fidelity towards breeding sites in the great cormorant. *J. Anim. Ecol.*, **69**: 214–223.
- Soldaat, L.L., Vetter, B. and Klotz, S. 1997. Sex ratio in populations of *Silene otites* in relation to vegetation cover, population size and fungal infection. *J. Veget. Sci.*, **8**: 697–702.
- Stephens, P.A. and Sutherland, W.J. 1999. Consequences of the Allee effect for ecology and conservation. *Trends Ecol. Evol.*, **14**: 401–405.
- Stephens, P.A. and Sutherland, W.J. 2000. Vertebrate mating systems, rarity and conservation. In *Vertebrate Mating Systems* (M. Apollonio, M. Festa-Bianchet and D. Mainardi, eds), pp. 186–213. London: World Scientific Publishing.
- Stephens, P.A., Sutherland, W.J. and Freckleton, R.P. 1999. What is the Allee effect? *Oikos*, **87**: 185–190.
- Sutherland, W.J. 1996. *From Individual Behaviour to Population Ecology*. Oxford: Oxford University Press.
- Székely, T. 1992. Reproduction of kentish plover *Charadrius alexandrinus* in grassland and fish-ponds: The habitat mal-assessment hypothesis. *Aquila*, **99**: 59–68.
- Treherne, J.E. and Foster, W.A. 1982. Group-size and anti-predator strategies in a marine insect. *Anim. Behav.*, **30**: 536–542.
- Van der Jeugd, H.P. 1999. Life history decisions in a changing environment: A long-term study of a temperate barnacle goose population. Doctoral thesis, Uppsala University.
- Zwarts, L. 1976. Density related processes in feeding dispersion and feeding activity of teal (*Anas crecca*). *Ardea*, **64**: 192–209.

