Research paper

Evolution of habitat selection: stochastic acquisition of cognitive clues?

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Abstract. Different habitat preferences in animals have been interpreted mostly as a result of different adaptive design of the species and/or as a result of interspecific competition. We propose an alternative view of evolution of habitat preferences. Our model is based on progressive stochastic acquisition of cognitive clues discriminating habitat features which correlate with expected fitness. We assume that acquisition of each cognitive clue allowing discrimination of 'better' and 'worse' habitats (according to the average fitness in each habitat) will constrain further evolution, because each further clue will discriminate habitats only within previously acquired preferences. Simple simulation model shows that if it is the case, even the species with equal habitat-related fitness differences will rapidly diversify in their habitat preferences. Therefore, similarly as in the evolution of other species-specific traits, the evolution of animal–habitat relationship may be strongly affected by stochastic events and historical contingency.

Key words: between-habitat distribution, birds, cognitive abilities, evolution, habitat selection, interspecific relationships, phytophagous insects, stochasticity

Introduction

Animal species differ in habitats they occupy. These interspecific differences have traditionally been interpreted as either (1) only a by-product of the physiological, morphological or bionomical interspecific differences (Leisler, 1977), or (2) a result of different evolutionary histories (i.e., of independent evolution in different areas and consequent specialization to different habitats), or (3) a result of the interspecific competition followed by subsequent specialization to optimal habitats (Rosenzweig, 1981). Explanations (1) and (2) have some limitations. There are important interspecific habitat differences in sibling species which do not differ morphologically, physiologically, and bionomically and explanation (1) is thus not sufficient in many cases. The different evolutionary histories, on the other hand, do not explain why the species should not adapt to common habitat types after they became sympatric, i.e.,

why different habitat requirements due to different evolutionary histories should be so conservative. The competitive explanation of interspecific habitat differences has therefore become the most popular. Different habitat preferences of species are mostly regarded as a result of a specialization toward habitats where individual fitness is not lowered by the competition with the other species.

Empirical observations of animal–habitat relationships, however, do not often fit predictions based on competition theory. Consider, e.g., the thoroughly studied relationships of bird habitat occupancy. The competition theory predicts, e.g., that interspecific overlap in the habitat requirements is to be minimized (Wiens, 1989). But although there are often significant interspecific differences in habitat requirements and the requirements are strongly species-specific, there is still a strong overlap in the distribution of even very similar species. For example, although the individual species of genus *Sylvia* and *Phylloscopus*, respectively, have strict (and relatively well known and predictable) habitat requirements (see, e.g., Cramp and Brooks, 1992), their spatial distribution overlaps considerably owing to the fact that the preferred features of habitat are not exclusive. Brosset (1996) reported that pairs of African sibling species are either parapatric or sympatric and within the sympatric sibling pairs some pairs differ in their habitat but some are ecologically unrecognizable. Therefore, the real pattern of habitat segregation of closely related species is variable and not fully explainable by interspecific competition.

There is some evidence indicating that habitat selection is based, contrary to the optimal foraging theory and optimization thinking, on the habitat features that are not apparently related to the expected fitness. Habitat requirements of many species seem to be based on simple superficial features of habitat, as is vegetation physiognomy or landscape patterns (Hildén, 1965; Partridge, 1978). For example the Black Redstart (*Phoenicurus ochruros*) prefers 'stony' terrain regardless of other habitat features – it inhabits bare mountaintops, small rocks, as well as human buildings. Similarly the Willow Warbler (*Phylloscopus trochilus*) strictly depends on middle heights of tree or shrub vegetation and inhabits low willow scrub as well as the dwarf pine vegetation on moorlands and dense young tree plantations (Cramp and Brooks, 1992). The distribution of individuals within these preferred habitat types could be very variable and unpredictable. Haila *et al.* (1996) suggested that the pattern of bird-habitat relationship may be habitat avoidance rather than habitat preference, i.e. birds avoid some habitat types but are not much selective among the non-avoided habitats. Contrary to the models based on the optimization thinking, an inter-annual variation in bird distribution within non-avoided habitat types has been observed (Haila *et al.*, 1996).
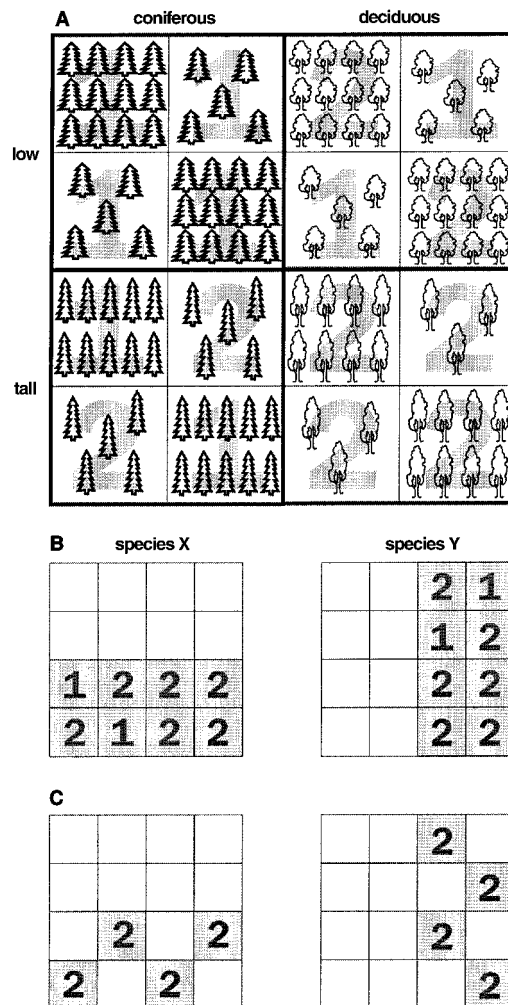
These phenomena may be interpreted as a consequence of limited opportunities for animals to optimize. Animals cannot directly estimate their future

fitness in any particular habitat patch. At the beginning of the breeding season, no direct information concerning important fitness-related ecological parameters (like *future* predation rate or food abundance) may be available (Partridge, 1978). Sometimes later colonising species may use earlier colonisers' presence as a cue to high quality patches (Mönkkönen *et al*., 1997, 1999). Sometimes, however, the valuation of the habitat quality must be based on indirect 'clues', i.e. on certain habitat features that are but correlates of factors causally related to the expected fitness. These clues can be constrained by the cognitive abilities of the animals as well as by historical contingency. Here we propose a model explaining diversification of species' habitat preferences by the independent evolution of cognitive abilities to recognize the important habitat features. According to the model, the evolution of habitat separation need not be driven by interspecific competition, although the competition may play a role: it could modify fitness of individuals in habitats that are shared with individuals of the other species.

The theory

Let us assume a species living in a heterogeneous habitat where every patch is characterized by an average fitness value and by a few qualitative features that are in principle recognizable by animals. These features may be but need not be causally related to fitness values (as is, for instance, the presence of important resources). If the habitat selection is density-independent we could expect a progressive selection of patches with higher fitness values: individuals able to select the higher-fitness patches will be more advantageous. In the course of generations, the ability to select better patches will be fixed in the whole population. However, the fitness expectation is but correlative, i.e., based on recognizable features of the habitat. This correlation could be weak: there is a single evolutionary rule that in any step, 'selective' individuals must have a higher average fitness than the 'non-selective' ones. Acquisition of any clue allowing the occupation of higher-fitness patches is advantageous regardless of the causal relation between the feature and the fitness value. We could then suppose that the way of acquiring habitat clues is quite stochastic and unpredictable, as there is usually more than a single possibility to acquire a higher fitness value in each step.

Let us now assume two species living in the same heterogeneous habitat and having similar fitness values for each habitat patch (i.e. they do not differ in their habitat-related bionomics, morphology and physiology). Each species will acquire habitat clues in a step-by-step manner. However, since every step elevating the average fitness value is fixed and the habitat clues are merely correlated to the average fitness, individual species could acquire distinct sets of clues (Fig. 1).

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Figure 1. (A) Let us assume two sibling species of foliage-gleaning birds living in a woody habitat which is characterized by three parameters (each parameter has only two qualitative states): the type (coniferous or deciduous), density (high or low) and height (tall or low). Any combination could have one of two fitness values, 1 and 2; i.e. any combination is either 'poor' or 'good'. Let us assume, in addition, that tall deciduous wood is 'good', whereas low coniferous wood is 'poor' for the foliage gleaners. Moreover, within the low deciduous wood, dense patches are 'good', whereas in tall coniferous wood only thinner patches are 'good' due to, e.g., well developed understory. (B) When both species occupy all patches, their mean fitness is 1.5, but when the individuals restrict their habitat occupation toward the preference of only tall wood (species x) or only the deciduous wood (species y), their mean fitness will be higher (1.75 in both species). At this stage both species have distinct but overlapping habitat preferences. (C) In the next step they could both either specialize to tall and deciduous wood or they could diverge to a thinner wood (species x) and a denser wood (species y), respectively, to reach the mean fitness of 2. In the last case the species will have non-overlapping habitat preferences, though their fitness has been identical in all patches.

Moreover, as the species are more and more specialized (i.e. preferring a smaller part of the whole 'area'), the overlap of the areas they occupy will decrease. The species could, of course, converge toward habitat patches with the highest fitness value, but probability of this convergence is low because each discriminating step is constrained by the previous ones. Better patches are discriminated by any further step only within the already preferred habitats; any newly acquired clue operates only in combination with the other clues.

Such scenario of habitat specialization and between-species diversification would occur if specific conditions were met:

1. *Relatively low cost of searching for the preferred habitat.* If there were high searching costs, the animal distribution would be dependent on the meta-population processes and the spatial structure of the environment rather than on habitat type.

2. *Stable between-habitat fitness differences.* The fitness differences must not be balanced by density-dependent effect, as is, for instance, in the ideal-free distribution (Fretwell and Lucas, 1970). In the ideal-free distribution the advantage acquired by the occupation of the better habitat is perfectly balanced by a disadvantage due to higher population density in that habitat. The fitness is consequently equal in all habitat types and further habitat specialization does not occur.

    Stable between-habitat fitness differences are realized when (1) the inter-habitat distribution is despotic (Fretwell and Lucas, 1970), and more fit individuals occupy better habitats and actively exclude the other individuals, and/or (2) the habitats are not saturated, population abundance being not controlled by resource abundance in different habitat types.

3. *Limited possibility to 'test' habitat types other than the preferred ones.* If only some individuals occupy the preferred patches whereas the others are pushed out of them, the unsuccessful individuals could acquire other cognitive clues and simultaneously lose the previous one. If the population would have enough time to test all possible combinations of cognitive clues, it could finally reach the real optimum (if any) and different species could converge. This condition is most important. There are always some individuals who do not occupy the preferred habitat and consequently are able to test the other habitat clues. However, the behavior of these individuals is still constrained by their species-level preferences, and they, consequently, expand selectively to certain habitat types. Therefore, the animals are not able to test all possible combinations of the habitat clues and the possibility to reach global optimum remains limited. Moreover, owing to a too quickly changing environment, most species might still be in the process of habitat diversification and the real populations have never had enough time to reach the global or even the local optimum.

All three conditions may seem quite restrictive. In fact, however, evolution of habitat separation by interspecific competition depends on even more restrictive conditions (Wiens, 1989): interspecific competition could act only if intraspecific competition do occur, fitness of at least one species is lowered by reducing resource availability (i.e. populations are regulated by resource abundances) and if the role of indirect interactions is limited (i.e. within relatively closed and localized systems). Moreover, the three conditions of our scenario do not restrict operation of the process as a whole, but only further continuation of the process: the process could run as long as the conditions are fulfilled. Contemporary pattern of habitat preferences could represent just the state when further continuation of the process is not allowed because the conditions are not yet fulfilled.

The simulation model

In a simple simulation model, the habitat was represented by 2000 'patches'. Each of them was characterized by one random fitness value and ten 'habitat features', each of them with two possible states (randomly assigned 0 or 1). Model populations, initially occupying all the patches, have randomly acquired or lost the 'discriminant clues' for individual habitat features. This allows them to either restrict or expand the range of occupied patches according to the random change in the preference of some habitat feature (realized as acquiring a preference of state 0 or 1 for respective habitat feature, or as a lost of the preference in that feature). For every step of the 'evolution' of the habitat discrimination, the average fitness of the occupied patches was calculated. When the average fitness was higher than the fitness in the previous step, the recently acquired clue was 'fixed', and the process continued. When the fitness was not elevated, the previous state was maintained. The process stopped when no change led to a higher average fitness.

Results of the simulation are presented in Figure 2. In all simulation experiments, the range of occupied habitats has restricted rapidly. Moreover, the habitat overlap between two populations has narrowed even more rapidly. Every pair of populations became completely separated very early. Finally, different populations inhabit completely different habitat patches although their initial conditions were identical and all the steps were linked with the increasing fitness. Most of the 'successful' changes led to the restriction of the habitat range, although the probabilities to acquire or to lose the habitat clue were equal.

The model is as simplified as possible and it is, consequently, quite unrealistic: it presupposes, for instance, that individual habitat features are not correlated (or are randomly correlated) and that the species could restrict their
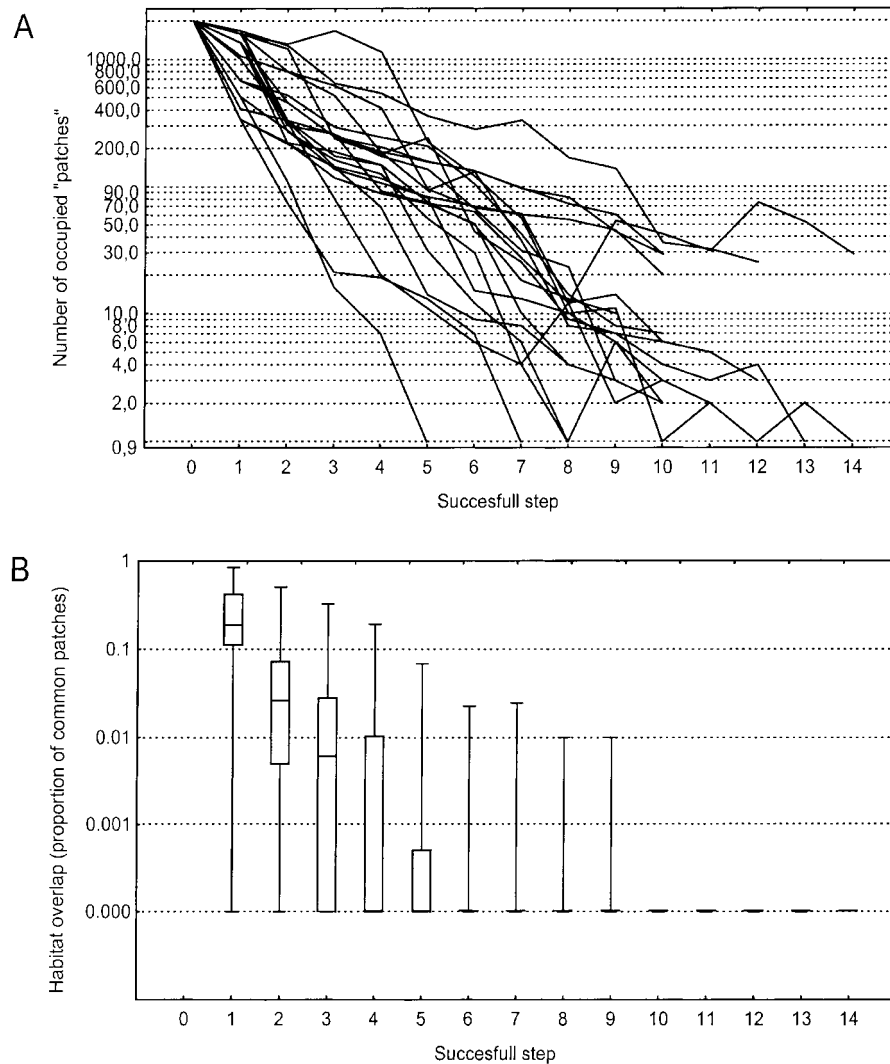
Figure 2. Results of twenty independent simulations. (A) Development of the range of the occupied patches in each 'species'. A restriction of the occupied 'habitat' is usual although there are also minor exceptions. (B) The ranges (median, 25% and 75% percentiles, min, max) of all overlaps between all 'species' pairs in each successful step. The habitat overlaps between species converge to zero. Note: y-axis is in the logarithmic scale. The zero value of the overlap was replaced by 0.2 for this purpose.

habitat ranges *ad infinitum*. It is probable that if habitat parameters are at least partly correlated and if the species are not able to restrict their habitat preferences below some minimal occupied area, the habitat ranges would not be so narrow and some interspecific habitat overlap would occur.

Applicability of the model

Our model provides an explanation of natural patterns of inter-habitat distribution in rather specific situations due to the restrictions mentioned above. Generally, our theory could be reliable in the situations where habitat is selected using some simple clues and a role of intraspecific and/or interspecific competition is reduced. Some taxa seem to be particularly prone to the evolution of habitat selection by progressive acquisition of cognitive clues. Perhaps the best candidates are birds selecting particular habitat type and phytophagous insects selecting particular host plants, for following reasons:

1. Both birds and insects fly and their searching for habitat often requires no extra energetic costs. Although there may be some costs related to the time-delays at the onset of breeding (especially in birds), these costs may be relatively low in such mobile animals. Therefore, the first condition mentioned above is fulfilled in these groups.
2. Both groups often do not follow the ideal-free distribution. Many birds are territorial with despotic inter-habitat distribution (Patterson, 1980; Parker and Sutherland, 1986). There is also evidence that bird population densities are controlled by factors not linked to resource abundance during the breeding season (Sinclair, 1989; Sæther *et al.*, 1996). The key factors are related mainly to overwintering, migration etc. Accordingly, the breeding habitats are not saturated, populations do not reach carrying capacity, and no density-dependent effect should take place. Phytophagous insects, on the other hand, also often do not reach the carrying capacity and interspecific as well as intraspecific competition seem to be limited there (Strong *et al.*, 1984). Therefore, in these groups the second mentioned condition is often fulfilled.

The general validity of our model could be tested by intertaxonomic comparison. Territorial species of birds should be, for instance, more prone to the evolution of habitat selection by progressive acquisition of cognitive clues, because they follow despotic distribution with its stable between-habitat fitness differences. Similarly, sibling species that depend on resources whose presence and abundance is not known in the time of territory establishment (e.g. prey abundance) should differ to each other in habitat selection, because they might acquired habitat preferences representing different correlates of their expected fitness. These differences should be more pronounced also in species whose habitat preferences are heritable, because species that select their habitats according to past experience or philopatry should converge. However, testing all these predictions may be very complicated due to the problems with exact measurement of species' habitat restrictivity. The question of applicability of

our model to the contemporary changes in habitat selection accompanying human-induced environmental changes remains open as well.

Concluding remark

According to Rose and Lauder (1996), evolution can be regarded as a highly stochastic process, which is strongly affected by historical contingency. On the other hand, species-habitat relationships are usually viewed as relatively predictable phenomena resulting from a simple optimization process (Rosenzweig, 1981). Our model shows that the evolution of habitat preferences could be as stochastic as the evolution of other species-specific traits. Different habitat requirements of species are not necessarily the consequence of their different fitness responses to habitats, but the consequence of a stochastic acquisition of habitat preferences constrained by history. Therefore, a single adaptive design may result in several trajectories of adaptive evolution leading to the acquisition of habitat preferences.

Acknowledgements

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