How can maladaptive habitat choice generate source-sink population dynamics?

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Several theoretical models have been proposed to describe population dynamics in a spatially heterogeneous environment. The source-sink model is among the most popular. Diffendorfer recently summarized its assumptions and predictions. Given the model reviewed, he argued that source-sink population dynamics arises if dispersal is somehow constrained. I offer an additional mechanism by suggesting that source-sink population dynamics can be generated by anthropogenic changes in landscapes that occur so quickly that organisms no longer make optimal habitat selection decisions. Individuals select the same habitats as their ancestors but these decisions no longer provide high fitness because of human-induced changes in habitat quality, such as increased rates of predation and/or parasitism. Provided that some of the habitats selected are turned by human-induced changes into sink habitats, source-sink population dynamics can emerge.

Habitat heterogeneity in a spatial, landscape context is an important issue in contemporary ecology (Blondel and Lebreton 1996). Individual habitat patches can be of varying suitability for growth, survival and reproduction of individuals and these differences have consequences for their population dynamics. Many population models based on different assumptions and leading to different predictions have been proposed to account for the population dynamics in heterogeneous landscapes (Kareiva 1990). Among the most popular, the source-sink model (Holt 1985, Pulliam 1988) assumes habitat patches of highly varying quality. In sources natality exceeds mortality and they are net exporters of individuals whereas in sinks mortality exceeds natality and they are net importers of individuals. This model predicts a net flow of individuals from sources to sinks (or to pseudosinks sensu Watkinson and Sutherland 1995; reviewed in Dias 1996).

It may be rewarding to consider population models in terms of an individual's behavioural decisions (Łomnicki 1999). There is no benefit for an individual to select a habitat where mortality exceeds natality. This logic stems from the ideal free distribution model of Fretwell and Lucas (1970). Then, for source-sink population dynamics to arise, we should explain why an individual would arrive at a habitat where mortality exceeds natality, i.e., at a sink. Three possible mechanisms have been proposed, all of them involving some constraint on dispersal: 1) passive dispersal (e.g., wind or water dispersal of propagules forcing individuals to grow and reproduce in a poor habitat), 2) territoriality, or despotic distribution (in active dispersers dominant individuals can exclude subordinates from good habitats thereby forcing them to live in poor habitats; Dias 1996, Diffendorfer 1998), and 3) temporal barrier (preventing successful colonisation of otherwise suitable habitat; Boughton 1999).

For a better understanding of the subsequent reasoning, two facts should be stressed. First, habitat selection can be viewed as a two-stage process. On the proximate level, an individual selects, through an interaction of its preferences with environmental cues, a part of the environment that becomes its habitat. The appropriateness of these behavioural decisions involved in the selection process is evaluated by natural selection on the ultimate level (Fretwell and Lucas 1970). Phenotypes possessing the best habitat selection rules (judged in practice by some appropriate correlate of fitness) produce most offspring. A prerequisite for this mechanism to allow animals to adapt is a long-term correlation between cues used by individuals while selecting habitat and the real suitability of that habitat. Second, organisms are adapted to their past environments. Nat-

ural selection is backward, not forward looking and the usefulness of an individual's adaptation is dependent on the temporal "sameness" of its environment (Freeman and Herron 1998: 45).

Anthropogenic changes in landscapes

Habitat fragmentation generally results in a landscape consisting of remnant areas of native vegetation surrounded by a matrix of agricultural or other developed land. Typically, it is characterized by loss of the original habitat, reduction in habitat patch size, and increasing isolation of habitat patches (Andrén 1994). The effects of habitat fragmentation can lower the quality of fragmented habitats, potentially generating source-sink population dynamics (Donovan et al. 1995, Robinson et al. 1995). These effects include increased nest predation and parasitism rates a) on habitat edges and b) inside remnant patches of native habitat.

The ecological trap hypothesis was originally developed by Gates and Gysel (1978) to account for maladaptive nest-site selection by open-nesting passerines on abrupt forest-field edges. The argument goes as follows: birds, especially small passerines, are expected to select highly concealed nest sites to avoid nest predation (Martin 1993). Modified dense vegetation at edges can exploit these habitat preferences and function as a (supernormal, see Manning and Dawkins 1998: 143) stimulus soliciting settling response and attracting birds to breed. This leads to overcrowding of nests in edge vegetation and can enhance, through density dependence, nest predation and parasitism rates (McCollin 1998). Birds breeding in/near edge vegetation consequently suffer from poor breeding performance (reviewed in Paton 1994). Such a habitat can become a demographic (pseudo)sink.

Besides creating abrupt vegetation edges, habitat fragmentation has a negative impact on forest-interior birds through increasing the intensity of predation pressure on their nests inside remnant patches of native habitat (e.g., Andrén 1992, Donovan et al. 1995). Increased nest predation can be explained by a landscape-wide increase of generalist predators supported by a matrix of highly productive agricultural land (Andrén et al. 1985). The increase in generalist predators must outweigh the decrease in forest-interior predators to result in rising predation rates in fragmented forests. Where the matrix ecosystems are not capable of supporting generalist predators (Donovan et al. 1997), or when we are concerned with naturally scattered habitats (Tewksbury et al. 1998), the effect of an increased overall predation pressure is absent. Another mechanism which can combine with that outlined above is a mesopredator release, i.e., an increase in the abundance of small omnivores (= mesopredators) in the absence of human-exterminated top predators (large canids and felids). The mesopredators can induce high predation pressure on open-nesting passerines (Rogers and Caro 1998, Crooks and Soulé 1999).

Negative effects of nest predation can be further strengthened by increased intensity of brood parasitism in fragmented landscapes (Trine et al. 1998). Human-caused changes in landscapes resulted in cowbirds (brood parasites) expanding their ranges and using new host species. In particular, the fragmentation of forests and the spread of animal husbandry in North America over the past 150 years appear to have favoured cowbirds (Cruz et al. 1998).

Habitat selection is a hierarchical process and migratory birds encounter multiple stimuli on their journey from the wintering grounds (Cody 1985). Deterioration of habitat quality through habitat fragmentation can certainly occur on several spatial scales. On these different spatial scales different processes occur while birds are approaching their breeding grounds. At larger spatial scales site tenacity and species-specific natal/breeding dispersal may be important while at finer spatial scales habitat selection controlled by specific stimuli is more important. With the help of such hierarchically occurring processes birds can be led to forest fragments not being aware of their poor quality caused by recent human disturbances (extermination of top predators, maintenance of highly productive surrounding matrix, see above) because there are no stimuli they can use to assess the poor quality.

In summary, a potentially strong effect of habitat fragmentation is the deterioration of the link between the cues used by animals for making habitat selection decisions and the qualities of those chosen habitats. If these habitats are recently created sinks, then source-sink dynamics can emerge. The most important thing, however, is that these changes come too quickly for animals to be able to cope with them (see Holt and Gomulkiewicz 1997, and references therein, for prerequisites for adaptive evolution in sink habitats, Thompson 1998 for examples of rapid evolution).

Conclusions

Current models of source-sink population dynamics (summarized by Diffendorfer 1998) propose constraints on dispersal (territoriality, or despotic distribution in active dispersers) as the only mechanism causing source-sink dynamics because individuals are unable to achieve all possible dispersal patterns. I suggest that human-induced alterations of natural habitats can have the same effect: either through providing animals with novel cues which they misinterpret as signals of high-quality habitats (abrupt edges), or through connecting cues used as indicators of good habitats with poor

fitness rewards (elevated predation and parasitism rates inside forest patches).

The two approaches – the traditional approach (i.e., territoriality, or despotic distribution) and maladaptive habitat choice approach – should generate different predictions to be testable and separable. Whereas the despotic distribution predicts that animals should in the first instance select the best habitat and as these are filled poor ones, the main prediction of the maladaptive habitat choice hypothesis is that animals should first select a poor habitat (the other two predictions, namely that poor habitat is a true sink and that there is a net flow of individuals from sources to sinks, are common to both approaches and are readily testable with the use of standard methods). There are several ways to show that individuals prefer a poor habitat to a good one. Either directly – animals should settle, after arrival on the breeding grounds, at first in a poor habitat (i.e., we can use a temporal settling pattern), or indirectly – individuals in a poor habitat are to be bigger (Dias and Blondel 1996) or to have better developmental stability (Møller 1995). Since the indirect approach assumes that competitive abilities of individuals are identifiable from some of their phenotypic traits, the direct approach is superior. However, the direct approach is unfortunately applicable only for migratory animals.

What is important to realize is that dispersal constraints and maladaptive habitat choice are completely different mechanisms. Previous models of source-sink dynamics assume that animals are able to correctly assess habitat quality but they cannot for some reason settle in a good one. Diffendorfer (1998) argues that in organisms with active dispersal, which can assess habitat quality and make decisions regarding whether to stay or leave, source-sink dynamics should not appear because it makes little evolutionary sense for an individual to remain in a sink habitat. He suggests that such individuals will be rarely found in poor habitats because they can assess poor quality and avoid it. On the contrary, I assume that animals make, using cues that worked well in the past, bad habitat selection decisions. This scenario is most plausible in habitats that have changed so rapidly that natural selection has not yet reshaped habitat choice. Consequently, we could find source-sink population dynamics even in active dispersers living in human-altered habitats (as might be the case in North American forest-interior passerines, Donovan et al. 1995, Robinson et al. 1995).

On the other hand, purely ecological processes can be responsible. For example, population fluctuations (Dunn 1977, Hogstad 1995), range expansions (Rogers and Caro 1998), fires and storms all change the strength of biotic interactions; this can result in changes in quality of some habitats, with the potential consequences for population dynamics outlined above. I focused on habitat fragmentation because it is rapidly ongoing, the best studied and currently the most important factor influencing species' habitats.

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