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S10-5 Demographic responses to habitat fragmentation

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Abstract Destruction of natural habitats involves two different, commonly simultaneous changes in the landscape: habitat loss and habitat fragmentation. Fragmentation effects can compound the negative effects of habitat loss on bird populations. We provide an analytic overview of numerical and demographic responses in bird populations to habitat fragmentation. We also survey measurements that can be taken from populations to help reveal key mechanisms behind bird responses to habitat fragmentation. We conclude that studies on demographic responses of birds to habitat fragmentation would be more effective if based on measures that are selected beforehand to distinguish among mechanisms and which can be taken with ease. Finally, we review relevant literature to evaluate what has been measured. Nesting success is the most frequently taken measurement, reflecting the recent emphasis on nest predation and parasitism in fragmentation studies. In contrast, we found no study where the relationship between population sex ratio and habitat fragmentation has been examined. Far-reaching conclusions cannot yet be made because of publication bias and nonrandom selection of species and landscapes for studies.

Key words Fecundity, Nest success, Patch size effect, Reproductive output, Survival

1 Introduction

Recent rates of extinction of known animal and plant species, from diverse environments in diverse regions, are 100 to 1000 times greater than their prehuman levels. The prime reasons for this decline are indisputably anthropogenic (Pimm et al., 1995), in which habitat loss and fragmentation are preeminent factors (Rappole, 1996).

Destruction of natural habitat involves two different, generally simultaneous changes in the landscape. One, and perhaps the more important, is the loss of original habitat via proliferation of disturbed and man-made environments (Pimm et al., 1995; Schmiegelow and Mönkkönen, 2002). The other, which invariably accompanies habitat loss, is the decrease in patch size of habitat remnants. Patch size reduction translates into increased exposure at patch edges and increasing levels of patch isolation (Andrén, 1994).

It is important to distinguish between the effects of pure habitat loss and fragmentation. When habitat is lost from the landscape, the individuals inhabiting it are lost too, resulting in population declines. In circumstances of habitat loss alone, without fragmentation effects, there is a linear relationship between the number of individuals and the area of habitat, so that the density of individuals per unit area remains constant. Fragmentation effects (patch size reduction and isolation) can exacerbate the effects of pure habitat loss, potentially producing even greater population declines (Andrén, 1994; Bender et al., 1998). This may ultimately result in population extinction even if suitable habitat still remains. Major declines in species richness follow, at least in tropical (Gascon and Lovejoy, 1998) and temperate (Donovan and Flather, 2002) regions.

We have indirect evidence on numerical responses of birds to habitat fragmentation through numerous studies of patch size effects, all of which point to reduced density in small patches. Bender et al. (1998) and Connor et al. (2000) reviewed such studies, the former concluding that patch size effects were strongly negative for bird species associated with habitat edge (decreased densities with increasing patch size), but strongly positive for bird species specialized to habitat interiors (increased densities with increasing patch size). This indicates that for interior species, declines in population size resulting from habitat fragmentation will be greater than predicted from simple habitat loss alone. Several studies have also shown that avian numerical responses to patch size effects are sensitive to landscape context, i.e., the type of disturbed habitat in which patches of original habitat are embedded (Mönkkönen and Reunanen, 1999; Norton et al., 2000; Ricketts, 2000).

Despite wide knowledge of the numerical effects of habitat loss and fragmentation on bird populations, our understanding of the mechanisms causing these responses is far more limited. Proper understanding of such mechanisms is crucial because only then can we start taking effective steps to remedy the negative effects of fragmentation. In this paper, we provide a flowchart linking landscape changes to demographic and numerical responses. We then proceed with an analytic survey of the measurements that can be taken from populations to help reveal key mechanisms behind responses to habitat fragmentation. Finally, we review the existing literature to evaluate what has been measured.

2 From habitat fragmentation to demographic effects to abundance patterns

We address here true fragmentation effects, i.e., changes in bird populations resulting from patch size, patch isolation and patch-edge effects. We do this because habitat loss alone does not result in changes in the demographic parameters of populations. Accordingly, we focus on three different demographic components: (i) annual survival rate, (ii) fecundity (or clutch size), covering total investment by a female or a pair in the clutch during one breeding attempt, and (iii) reproductive output or nesting success, i.e., the rate or probability with which fecundity is transformed into independent offspring.

Mechanisms affecting these components fall into three categories. First, predation upon adult birds and their offspring (nest predation) may have a strong impact on population demography, particularly annual survival and nesting success. Several studies have shown that landscape change can result in dramatic changes in predator species assemblages, overall density of predators and predation pressure on birds and their nests (Andrén, 1992, 1995; Bayne et al., 1997). Secondly, habitat fragmentation may in many ways affect the availability of critical resources such as food. According to the "resource concentration hypothesis" (Root, 1973), there is a greater concentration of critical resources in larger habitat patches, resulting in higher population densities of consumers. Thirdly, fragmentation may disrupt functional connectivity in the landscape, causing problems for dispersal and movement. For example, some patches in the landscape may become unreachable if too isolated from other patches, thereby lowering the chances of meeting and pairing success (Cooper and Walters, 2002).

We argue that avian numerical responses to fragmentation stem mostly from the above demographic components. If survival, fecundity and/or nesting success are negatively affected by fragmentation, population size will certainly decline more than would be expected from habitat loss alone. Numerical responses may also result from demographic effects anticipated by birds themselves, for example in cases where they respond adaptively to landscape changes by deserting small habitat patches. It is important to distinguish between population-level and individual-level mechanisms here, even though their effects are commonly parallel (Andrén, 1994). Individual responses can be seen as proximate processes, while population responses are ultimate and more directly linked to population persistence.

3 Measurements and mechanisms

There are several alternative ways, both direct and indirect, of measuring each of the components of population demography. Individual survival can be measured directly by mark-recapture or indirectly through annual turnover of individuals. Fecundity can be measured directly by clutch size or indirectly by the timing of nesting, which is related to clutch size (Godfray et al., 1991). Pairing success and population sex ratio are also important components of fecundity. Moreover, rates of nest predation and parasitism, as well as the number of fledglings and their quality, are further measurements associated with nesting success. Such measurements can also be divided into those that are taken from adult birds (e.g., survival, pairing success, sex ratio) and those taken from nests (e.g., clutch size, rate of nesting success).

The mechanisms listed above also have both direct and indirect effects on population demography and on the measurements we take from populations. For example, predation directly affects annual survival, but may indirectly influence sex ratio or age structure if predation is either sex- or age-biased. Nest predation has direct effects on both nest success rate and population age structure, and may indirectly affect site fidelity as well, thereby modifying annual turnover in local populations.

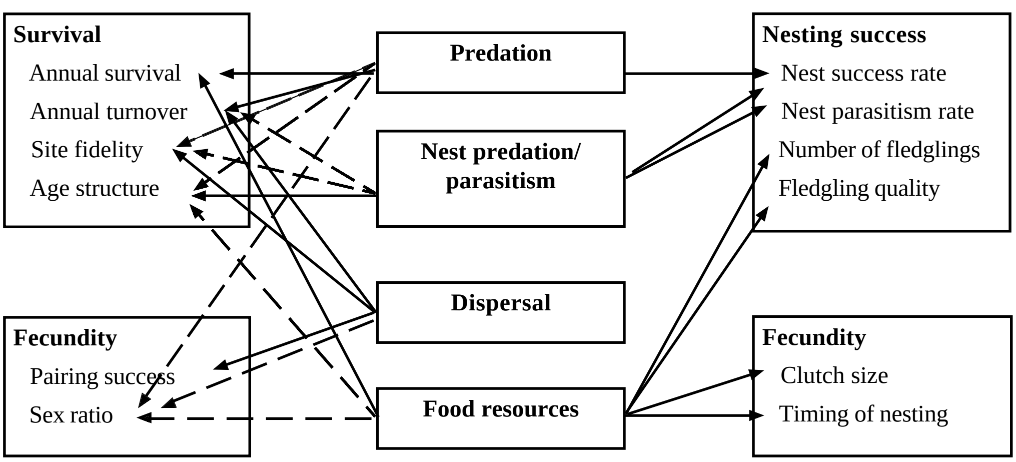

Fig. 1 Measurements of bird population demography that can be taken from adult birds (left) and nests (right)
Mechanisms are itemized in the middle of the diagram against direct (solid arrow) and indirect (dashed arrow) effects on measurements.

One potentially important message emerges from the direct and indirect links between mechanism and measurement. It is embodied in Fig. 1, which suggests that a clearer understanding of important processes affecting population demography can be gained from inspecting nests. Here the mechanisms that may be considered putative factors for demographic change in measurements that can be taken from nests are narrowed, as a rule, to one.

The various measurements can be ordered according to their ease of acquisition. It is relatively easy to assess population densities, because of which much is already known about numerical responses. Unfortunately, measurement of density alone does not allow us to draw conclusions about the mechanisms causing numerical responses. Pairing success, timing of nesting and fecundity (clutch size) are also relatively easy to measure because they only require one or several observations. Nest success and fledgling quality (e.g., mass, growth rate and body condition of fledglings) do require more detailed monitoring of nests, but are still more easily taken than those that require the capturing of adult birds one (sex ratio, age structure data) or more (annual survival, site fidelity data) times. Fledgling quality reflects the effects of resources but is only slightly, if at all, affected by predation.

We conclude that most effective and efficient studies on demographic responses to habitat fragmentation in birds are those that have used measurements that can be taken most easily, with the caveat that planning should be undertaken beforehand to select those measures that distinguish among mechanisms. A good combination of non-experimental measurements would be pairing success, nest success rate and fledgling quality monitored simultaneously. Here pairing success is likely to be affected only by dispersal; and nest success and fledgling quality can be used to distinguish between the effects of predation and resources. Other similarly optimal combinations can be found by inspecting Fig. 1.

4 Literature review of demographic response to fragmentation

We conducted a literature search in the BIOSIS database for studies dealing with forest bird responses to habitat fragmentation. For this, we used a combination of keywords given in Fig. 1 and included only studies dealing with forest fragmentation and demographic responses of birds in natural environments. All studies using artificial nests sites were thereby excluded. Two types of studies were found: those that provided data on demographic responses to variation in patch size, and those that compared bird demography in fragmented vs. unfragmented landscapes. For the purposes of this review, we pooled both types of studies. Altogether, 36 studies were found, with information on responses for 80 species. By *response* we mean one measurement (e.g., clutch size) for one species. Some studies provide data on one measurement for several species, while others gave information on a combination of measurements for one species population.

On average, measurements given for populations were scarce (mean = 1.4 measurements). Thus no firm conclusions about causal mechanisms for observed patterns could be made because, as we have shown, several measurements are needed to distinguish among mechanisms. Moreover, no studies on the relationship between sex ratio and habitat fragmentation were found (Table 1). By and large, the most frequently measured parameter was nest success. This probably reflects the popular belief that nest predation and parasitism are the primary causes of demographic change in fragmented landscapes. It is notable that almost two thirds of the studies found that fragmentation had either no effect on nest success (54% of cases) or was positive, i.e., nest success increased with increasing fragmentation (12%). No study detected a significant effect on clutch size, but other fecundity-related measurements, particularly pairing success, were found to be affected more frequently.

Dispersal was also implicated as an important mechanism because dispersal-related measurements (direct dispersal, pairing success) were found to be more frequently influenced by fragmentation than, for example, resource related measurements such as clutch size or fledgling quality. Such conclusions, however, may be premature because the data that we reviewed could have been biased in at least two ways. First, there could have been publication bias, whereby only papers submitting significant results were accepted for publication. Secondly, and perhaps more importantly, researchers may have selected species and

Table 1 Frequency of the responses of species of forest birds to habitat fragmentation according to a compilation of published studies

Fragmentation effect	Pairing success	Nest timing	Clutch size	Nest success	Fledgling quality	Sex ratio M/F	Age structure A/J	Annual survival	Dispersal
Negative	8	3	0	9	3	0	1	4	7
No effect	4	7	10	14	4	0	1	2	0
Positive	0	0	0	3	0	0	0	0	0
Number of studies	11	8	8	19	6	0	2	3	5

The demographic variables given from left to right are in order of decreasing ease of measurement. Each cell records the number of cases where effects were found. The bottom row gives the number of studies furnishing information for each demographic parameter. Note that the numerical results in each column may exceed the sum of studies because each study may provide more than one estimate.

measurements expected to reveal significant results, thereby creating their own bias. Thus, the species selected for expensive studies of dispersal were not chosen randomly. That all seven recorded cases in our review revealed that fragmentation had a significant, negative effect on dispersal should thus come as no surprise.

5 Discussion

Even though much is known about the numerical responses of birds to habitat fragmentation, we lag far behind in our understanding of the mechanisms involved and can therefore provide little knowledge on how to remedy impacts on populations at the landscape level. A good starting point for research to address this gap would be to focus on simple and readily measurable parameters such as pairing success, nest success and fledgling quality. To provide more robust assessments of demographic mechanisms, we propose that future studies should take an analytical approach to mechanisms and related measurements by repeating an exercise, such as that depicted in Fig. 1, which would pinpoint key variables. Assuming that each measurement has a cost, one should try to find a combination of measurements capable of distinguishing among such putative mechanisms as predation, resource availability and dispersal.

We also have very little understanding of adaptive responses to habitat fragmentation. For example, life-history theory (e.g., Stearns, 1992) and a large body of empirical research (e.g., Reznick et al., 2000) suggest that there are trade-offs among demographic traits. Allocation of more resources to one particular activity, such as reproduction, will result in less time and energy for other activities, for example, improvement of individual survival. The ultimate impact of habitat fragmentation on population viability is the result of not only changes in demographic parameters related to survival and reproduction but also in their trade-offs. This stresses the point that it is important to study all parameters affecting population demography (survival, fecundity and nest success) simultaneously if a sound, holistic understanding of population viability prospects in fragmented landscapes is to be achieved.

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