

DIVERSE EFFECTS OF FOREST FRAGMENTATION ON A NUMBER OF ANIMAL SPECIES

by

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SUMMARY

Since 1990 we have initiated a number of studies on the population ecology, population genetics and social organization of several animal species in forest fragments of varying sizes. Study species include squirrels, small passerines and butterflies. Study sites are forest fragments between 1 and 40 ha, and study plots in «continuous» forest of 100 to 1500 ha. Our results so far suggest that forest fragmentation has more profound effects on dispersal patterns and population structure than on reproductive output and survival. Effects on dispersal include at least two aspects, which are not necessarily found in the same species. First, immigration deficits may be caused by low disperser success and/or source-sink effects. Second, reduced gene flow among local populations may result in genetic differentiation and/or loss of genetic variation. Negative consequences of the latter are not obvious, but indirect effects may be important *e.g.* for local adaptation. We conclude that studies on population structure in fragmented habitats should include quantitative (dispersal distance, immi/emigration, genetic structure) as well as qualitative aspects (timing of dispersal, habitat selection).

Keywords : habitat fragmentation, gene flow, dispersal, demography.

INTRODUCTION

Habitat fragmentation has been recognized as a major threat to the survival of natural populations and the functioning of ecosystems. The reduction of large, more or less continuous habitats to small and isolated remnants affects the abundance and species composition of various taxa. Possible factors contributing to this decline include changes in predation or food availability, microclimatic effects, loss of genetic variation and lack of recolonization following local extinctions (see reviews by *e.g.* WILCOX and MURPHY, 1985, SOULÉ, 1986, OPDAM, 1991, SAUNDERS *et al.*, 1991). Given the extensive temporal and spatial scales on which these effects operate, true experimental studies are relatively scarce (LOVEJOY *et al.*, 1986, MARGULES, 1992, ROBINSON *et al.*, 1992, IMS *et al.*, 1993) and most in-

investigators have concentrated on horizontal comparisons of historically fragmented habitats.

Since 1990 the Laboratory for Animal Ecology of the University of Antwerp has initiated a series of studies on the population ecology, population genetics and social organization of animal species from different taxa in forest fragments. The aim is to investigate whether populations in highly fragmented habitats function differently compared to continuous habitats, which mechanisms are responsible for these differences, and how these affect the status of the population. We chose to study common species, not particularly endangered, that vary in dispersal capacities, abundance and trophic level. Here we report on some of our major findings thus far, and try to present some general conclusions that can be made at this moment.

STUDY SPECIES, STUDY AREAS AND GENERAL METHODS

Our studies so far include one mammal (Eurasian red squirrel *Sciurus vulgaris* L.), four small passerines (nuthatch *Sitta europaea* L., crested tit *Parus cristatus* L., great tit *P. major* L., blue tit *P. caeruleus* L.) and one butterfly (winter moth *Operophtera brumata* L.). All species are largely restricted to mature forest (Table 1). Crested tits are restricted to coniferous forest, squirrels prefer conifers but occur in broadleaved forest as well, and the remaining species prefer broadleaved forest and reach their highest abundance in forest dominated by oak *Quercus robur* L. All species are studied in a set of patches of secondary forest or parkland (henceforth «fragments») surrounded by agricultural land, sometimes partly by residential areas. The range of fragment sizes covaries with the abundance of the species under consideration (Table 1). Additional study sites in larger forests (> 100 ha) vary in number from one to three per species. All study sites are situated in northern Belgium, in a radius of 50 km from the city of Antwerp.

Methods are generally based on individually marking a substantial sample, if not the majority, of the population in the study sites, the only exception being the winter moth. In 1993 we started a large-scale nestbox study for great and blue tit with standard nestbox densities in 12 fragments of varying sizes, all within a few kilometers of one another. This approach provides us with direct estimates of demographic parameters, including immigration and emigration. In winter moth and tits dispersal is estimated indirectly by the study of selectively neutral genetic variation. Genetic variation is estimated by DNA fingerprinting in squirrels (WAUTERS *et al.*, 1994a) and blue tits (VERHEYEN *et al.*, in prep.), and by allozyme electrophoresis in winter moths (VAN DONGEN *et al.*, 1994). For further details see LENS and DHONDT (1994), MATTHYSEN *et al.* (1995), NOUR *et al.* (1993), VAN DONGEN *et al.* (1994) and WAUTERS *et al.* (1994a, b).

TABLE 1

Results (in part preliminary) on demography and population structure of six animal species in relation to forest fragmentation. The table indicates the level of various parameters and processes in small and isolated fragments, as compared to larger and/or less isolated fragments (or sites in continuous forest). — no difference, ?? no or insufficient information. For further information see text and references.

Species	Red Squirrel	Nuthatch	Winter moth	Crested Tit	Great Tit Blue Tit
Forest type	All	Deciduous	Deciduous	Coniferous	Deciduous
Fragment sizes	15-60 ha	2-40 ha	0.1-10 ha	10-50 ha	0.5-10 ha
Abundance	lower	lower	lower ²	lower	— ³
Reproduction	—	—	??	—	—
Timing	less synchronous	earlier	less synchronous?	later ⁴	earlier
Survival/condition	—	—	lower mass	—	??
Philopatry ¹	higher	—	—	—	higher
Timing of dispersal	??	delayed	??	delayed	??
Net immigration	lower	lower	??	lower	—
Gene flow	lower	— ⁵	lower	??	lower ⁵
Genetic variation	smaller	??	smaller	??	??
References	Wauters <i>et al.</i> , 1994a, b	Matthysen <i>et al.</i> , 1995 Matthysen, unpubl.	Van Dongen <i>et al.</i> , 1994 Van Dongen, unpubl.	Lens and Dhondt 1994 Lens, unpubl.	Verheyen <i>et al.</i> , in prep. Matthysen <i>et al.</i> , unpubl.

¹ proportion of surviving offspring that reproduce near the site of birth.

² not repeated in a second year (Van Dongen, unpubl.).

³ abundance mainly determined by nestbox availability.

⁴ second broods only.

⁵ estimated from local recruitment rates.

RESULTS

Table 1 summarizes the major findings in the six species under study. For more details we refer to the appropriate publications. In four of six species we found lower abundances in smaller and/or more isolated forests. In the winter moth this result is apparently less robust since it was not found in all years (VAN DONGEN, unpubl.). In great and blue tits population density is largely determined by nestbox density which we controlled. High nestbox densities in all areas (8 boxes per ha or more) resulted in overall high population densities. We found very little evidence for lowered reproduction, condition or survival in relation to fragmentation. Fledgling crested tits had a lower body mass in fragments, but the effect on their fitness is not clear, apart from delayed dispersal. Surprisingly, timing of reproduction differs between fragments and large forests in most, if not all species. In squirrels and perhaps winter moths reproduction is less synchronous in forest fragments; nuthatches, great and blue tits reproduce earlier in spring in fragments, and crested tits increase the interval between first and second broods.

Marked differences were found in dispersal patterns and/or population structure between populations in fragmented and unfragmented habitat. In general, two kinds of effects seem to exist, which are not necessarily congruent. First, in several species the degree of exchange with neighbouring populations is reduced, because of reduced emigration (*i.e.* a higher degree of philopatry) and/or reduced immigration. This implies reduced gene flow between populations and may result in genetic differentiation between local populations and loss of genetic variation. The latter was found in squirrels and winter moths. Second, a change in the immigration/emigration balance may result in a net immigration deficit. In fact, we believe that this immigration deficit may be the main reason why squirrels, nuthatches and crested tits are less abundant in forest fragments compared to larger fragments or continuous forest. Such immigration deficit can in theory be caused by two processes: either a higher loss of dispersers, or unbalanced immigration and emigration, *e.g.* net immigration in large forests and net emigration out of fragments. We have no direct evidence for either of the two, but found some qualitative differences, notably in the timing of dispersal and in habitat selection, that may give an indication on which process is responsible. In the following sections we will briefly review the results for each species.

Squirrel

Squirrel populations in forest fragments are characterized by a lower abundance, lower per capita immigration rate and a higher local survival of juveniles, compared to two large forests. Higher local survival probably indicates higher philopatry rather than true survival. The result is an apparent reduction in gene flow, since genetic variation is lower in fragments, and highly correlated with immigration rate. The increase in local survival is not sufficient to compensate for the loss of immigrants, and this may be the most likely explanation for lower population densities (WAUTERS *et al.*, 1994a). Observations on a small number of radio-

equipped juveniles show that they do not disperse far, and avoid crossing open areas (WAUTERS *et al.*, 1994b). Reduced breeding synchrony in fragments may be partly due to increased variation in the time when females reach the optimal condition for reproduction, and partly to females re-entering oestrus more rapidly after early nest loss (WAUTERS *et al.*, unpubl.).

Winter Moth

Winter moth populations in different forest fragments are significantly different in genetic composition. Moreover, genetic variation was reduced in the most isolated populations. In 1991 adult population densities were lower in more isolated fragments (VAN DONGEN *et al.*, 1994) but this relationship was not reproduced in 1993 (unpubl. results). Adult moths weighed less in genetically less variable populations (VAN DONGEN *et al.*, 1994). We currently investigate the hypothesis that because of reduced genetic variation in fragments, winter moths are less synchronized with host trees and therefore suffer in reproductive output.

Nuthatch

Juvenile nuthatches disperse over relatively large distances (several kilometers) between fragments, and philopatry is not higher in fragments compared to continuous habitat. Therefore we expect no difference in gene flow rates in fragmented or unfragmented populations. However, several lines of evidence suggest that dispersal is less efficient in and among fragments (MATTHYSEN *et al.*, 1995; MATTHYSEN and D. CURRIE, unpubl.). First, few first-year birds move to a different fragment after acquiring a territory, whereas territory shifts are common in a large forest. Second, new recruits arrive later in vacant territories in summer in the fragments, although potential recruits leave their parents at the same time in fragments and a large forest. Third, recruits seem less well able to select high-quality territories during their dispersal period, and fewer suitable territories are claimed. Less efficient dispersal and delayed recruitment may imply lower disperser survival, although we have no direct evidence for the latter. This in turn may explain the lower population density in fragments.

Crested Tit

All juvenile crested tits emigrated out of their natal areas, in fragments as well as a large forest. Hence we conclude, as in the previous species, that effects of fragmentation on gene flow are probably limited. However, juvenile crested tits delay their dispersal out of fragments compared to large forest plots. The reason may be a lower body mass at fledging, or a true barrier effect (reluctance to cross open spaces). Likewise, new recruits settle at a later date (on average) in fragments, but probably for a different reason. We suggest that fragments represent second-quality habitat, and therefore receive recruits that were unable to settle in large forests (LENS and DHONDT, 1994). Perhaps as a result, social winter groups were smaller in forest fragments and had larger group territories (LENS, 1994).

Great and Blue Tit

Preliminary results suggest that reproductive success is not lower in small forest fragments compared to larger fragments. Data on food provisioning at the nest similarly show no obvious differences in provisioning rate or diet composition between small and large fragments (NOUR and CURRIE, unpubl.). Although no quantitative analysis is as yet available, large numbers of recaptures of ringed birds suggest a high local recruitment rate in the fragments compared to larger forests, suggesting a high degree of philopatry. Gene flow between study areas is high but insufficient to prevent slight genetic differentiation as detected by minisatellite DNA single locus probes (VERHEYEN *et al.*, in prep.). In a previous study, DHONDT *et al.* (1990, 1991) found lower population densities and lower reproductive success in forest and park fragments around Ghent compared to study plots in and near a large forest in Antwerp. However, these results cannot be directly compared to the fragments in this study where nestbox density is lower.

DISCUSSION

The effects of habitat fragmentation – apart from the loss of suitable habitat – are manifold and have been addressed in an increasing number of studies. Some effects are now well documented, *e.g.* changes in predation level (*e.g.* ANDRÉN and ANGELSTAM, 1988, NOUR *et al.*, 1993), increases in the number of edge species (RANNEY *et al.*, 1981, JANZEN, 1983) and disappearance of species with high area requirements (*e.g.* ASKINS *et al.*, 1987, BIERREGAARD and LOVEJOY, 1989). These effects can be characterized in general as changing aspects of habitat quality. In this respect we find surprisingly little effect on reproduction and survival.

Nevertheless we document lower population densities of most species in smaller or more isolated forest fragments. It is noteworthy that all of these species have been confronted with fragmentation of their habitat for the past centuries, if not longer. Despite the lack of effects on reproduction and survival, our results do indicate possible routes for demographic effects. Notably, the winter moth which is an important food source during the reproductive period of tits and nuthatches (PERRINS, 1991), is affected by fragmentation: abundance seems to be lower and is probably more variable in fragments, and male moths weigh less. As the latter reflects reduced larval growth, this means that less biomass is available at the higher trophic levels. We currently investigate to what extent the food situation for the birds is really affected by the fragmentation-sensitive population structure of the winter moth.

Another suite of effects of habitat fragmentation can be characterized as changes in population structure through changes in dispersal patterns. As fragmentation proceeds, dispersal from one habitat fragment to another becomes more difficult. Many studies, especially theoretical investigations, have addressed the threats to the small populations resulting from the fragmentation of formerly large populations. The basic idea is that local populations become separated so widely that their demography and genetic dynamics become more independent of one another, which

may eventually lead to local extinctions and/or loss of genetic variation. For instance, metapopulation theory (GILPIN and HANSKI, 1991) predicts that smaller and/or more isolated populations have a higher chance to go extinct without being recolonized in the future, leading to a lower equilibrium level of extant populations, or even extinction of the entire metapopulation.

In our studies we find evidence that populations of squirrels and winter moths (and to some degree, blue tits) are structured into local populations with limited gene flow between them. Whether and how this population structure explains lower abundances is less clear, however. In squirrels, lower genetic variation is not correlated with lower reproductive success. In winter moths few data on fitness are available, and the effect on fitness may be rather complex through reduced synchronization.

However, effects on dispersal patterns may be more complex than reduced gene flow rates. In nuthatches and crested tits the average dispersal distance, and therefore the exchange between local populations, remains large in fragmented habitats. Nevertheless, some qualitative changes in dispersal are apparent: timing, habitat selection, and the immigration/emigration balance. It seems possible that these qualitative changes are accompanied by, or result in, a higher mortality of dispersers. Such an effect can decrease the viability of the entire fragmented population without apparent changes in dispersal distances or gene flow. It is noteworthy that nuthatches and crested tits share a year-round-territorial social system which forces young birds to disperse early in search of vacancies (MATTHYSEN *et al.*, 1995, LENS and DHONDT, 1994). In the squirrel both effects may operate: reduced dispersal, but also lower success of individuals that disperse.

Changes in habitat quality may also interfere with the dispersal pattern. In the crested tit there is a suggestion that fragments are second-quality habitat and therefore receive fewer immigrants. This possibility seems less likely in the squirrel where dispersal distances are short anyway (WAUTERS *et al.*, 1994b).

In conclusion, we suggest that effects of habitat fragmentation can be a complex mixture of changes in habitat quality and changes in dispersal patterns. Habitat selection and disperser success may be key factors in determining the fitness of a population in highly fragmented habitat. Therefore dispersal needs to be studied in both its qualitative and quantitative aspects. Once the population structure of a species is affected, this can have far-reaching consequences on their interactions with other species. For instance, winter moths with insufficient genetic variation may be incapable of synchronizing with their host trees; on the other hand, gene flow in tits may be too high to allow local adaptation to different food conditions (DHONDT *et al.*, 1990).

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