

# Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies

Paul Opdam

Research Institute for Nature Management, Department of Landscape Ecology, P.O. Box 46,  
3956 ZR Leersum, The Netherlands

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## Abstract

Metapopulations are conceived as spatially structured populations consisting of distinct units (subpopulations), separated by space or barriers, and connected by dispersal movements. Metapopulations characteristically demonstrate a turnover of local populations going extinct and becoming re-established, resulting in a distribution pattern that shifts over time. Metapopulation theory is used to analyse the effects of habitat fragmentation on birds in the temperate zone, integrating various explanations for the paucity of species in isolated ecotopes.

There is some evidence that turnover of local populations occurs in fragmented systems. A few studies based on time series demonstrate the local extinction rate to be related to the size of the habitat fragment, whereas the recolonization rate depends on the degree of isolation. Most evidence comes from short-term pattern studies in which the probability of occurrence was found to depend on the size of habitat fragments, on their relative position in the landscape and on the density of corridors lowering the landscape resistance. These data are consistent with predictions from metapopulation theory. However, almost all investigations consider wood fragmentation in agricultural landscapes, and there is a great need for studies in naturally fragmented landscapes as well as for studies focussing on other, less predictable, habitat types.

## 1. Introduction

Temperate forest landscapes have become fragmented over extensive parts of their original distributional range. Small patches of forest or other natural habitat are scattered throughout many agricultural landscapes (Forman and Godron 1984; Harms and Opdam 1989), leaving autochthonous species with the problem of how to survive in small populations, cope with deleterious effects of parasites, or predators intruding from the surrounding matrix, and cover the distance between patches.

Forest birds and occasionally marshland birds

have been the subject of many studies considering the effects of fragmentation of habitat due to the activities of man. Although in recent years reports from studies in tropical areas have begun to appear, the bulk of the literature considers fragmentation of temperate forest in North America and Europe (cf. Moore and Hooper 1975; Forman *et al.* 1976; Helliwell 1976; Whitcomb *et al.* 1981; Howe 1984; Ambuel and Temple 1983; Lynch and Whigham 1984; Opdam *et al.* 1985; Ford 1987; Wilcove *et al.* 1986; Van Dorp and Opdam 1987). The primary question addressed is: do small patches of habitat contain fewer species than larger ones, and why

would that be so? The literature does not provide a clear answer. Some authors claim that isolation is a causal factor, assuming that forest birds are **reluctant** to cross open land (e.g. Moore and Hooper 1975; Forman *et al.* 1976; **Helliwell 1976**; **Whitcomb *et al.* 1981**; Hayden *et al.* 1985; **Dickman 1987**). Others reject that explanation, referring to the long distances covered by migrants, and stress the interrelation between patch area and habitat heterogeneity: the larger the forest fragment, the more likely that a species will find its habitat (Williams 1964; **Freemark and Merriam 1986**). Still others stress the negative effects of nest predators and parasites, which lower the breeding success of forest song birds and, hence, contribute to their decline and local extinction (Ambuel and Temple 1983; Brittingham and Temple 1983; Wilcove *et al.* 1986; Small and Hunter 1988).

These explanations focus on individual patches rather than on entire landscapes, and usually tend to neglect interconnections among local populations in landscape fragments by dispersal flows of yearlings or (sometimes) adults. Such local populations become interdependent. Depending on the intensity of the dispersal flow through the landscape, local extinctions may be compensated by **recolonizations** or the dynamics of the local populations may be influenced so that extinction becomes less likely (the 'rescue-effect' of Brown and Kodric-Brown 1977). I will consider here fragmentation effects on the landscape level, and consider the local populations in fragments to form a multi-unit population, a metapopulation. Processes in the metapopulation are affected by the structure of the landscape (Opdam 1988, 1990a,b). The local dynamics of subpopulations are influenced by patch area, patch quality and the intrusion of negative factors from the surrounding landscape matrix. The dispersal flow depends on the configuration of landscape fragments: distance between habitat patches and the landscape resistance. Therefore, I take **metapopulation theory** as an interpretative framework to reconsider the evidence for the impact of fragmentation on forest birds. Most observations were made in agricultural landscapes with small forest fragments in the Northern hemisphere, so this landscape type will be somewhat overemphasized.

## 2. Metapopulation theory

Many papers dealing with fragmentation tend to neglect the fact that species are likely to differ in their response to the dissection of habitat. This is particularly striking in the SLOSS-discussion about the rationale to a choice among 'Single Large Or Several Small' nature reserves (McCoy 1983; **Soulé and Simberloff 1986**, among many others). Burkey (1989) argued that those focussing on maximizing species richness (neglecting species differences) claimed that a fragmented system can hold more species, whereas others focussing on minimizing extinction rate (species level!) reached controversial conclusions about preferable conservation strategies.

Clearly, fragmentation of habitat must have different effects for different types of species (Wiens 1989). For species restricted to the original vegetation type, the habitat is dissected into a number of smaller patches. The area in between is unsuitable or even inhospitable, and hence may act as a barrier or sink. This is the relevant group of species when talking about fragmentation as a threat to natural diversity. The other side of the coin is that this landscape change can be beneficial to those species depending on a mosaic of vegetation types. The edges of the habitat fragments may deviate in vegetation type and will contain particular edge species. Hence, the bird community of a forest consists of forest-interior species (the original inhabitants), edge species preferring the dense shrub layer of the forest edge or using the adjoining field for feeding (some of which may have occurred in natural disturbance patches in the original forest), and species breeding in the forest but roaming the whole mosaic of the surrounding landscape. Furthermore, the landscape will hold agricultural species.

The literature concentrates on negative aspects of man-caused fragmentation, *i.e.* the role of size and configuration of woodland fragments in the agricultural landscape. This emphasis, (which is usually not explicit) follows from the relatively high conservation value attributed to the remaining habitat in contrast to the intensively managed agricultural fields. I shall restrict this review to the negative effects of fragmentation, hence to those species

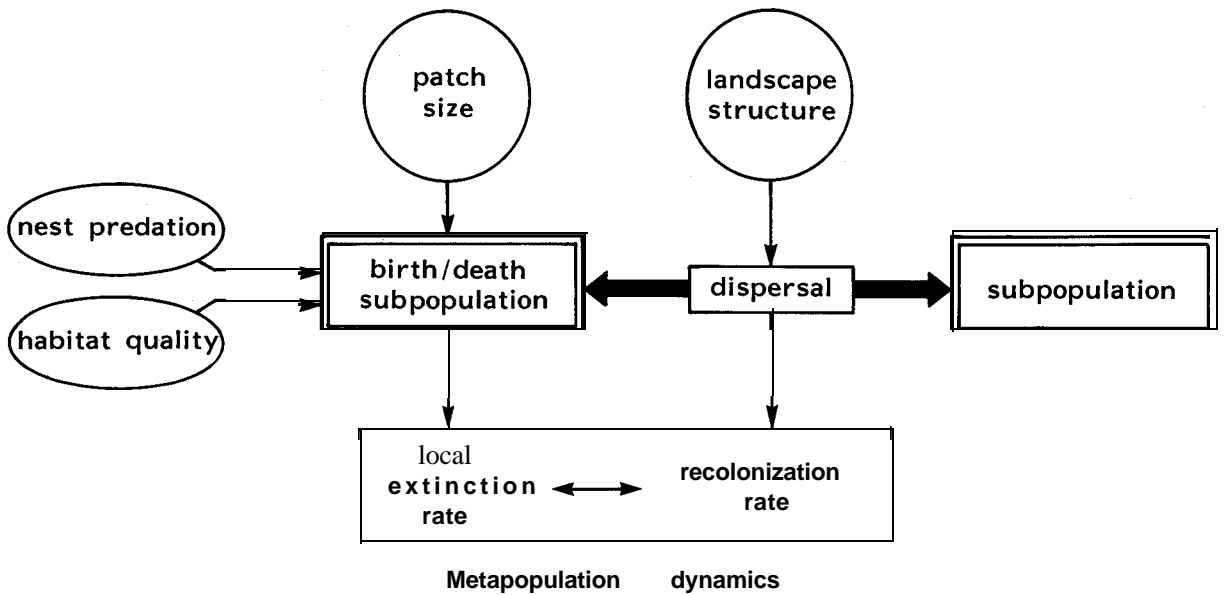


Fig. 1. Factors influencing metapopulation dynamics. The balance between local extinction and recolonization is determined by the local birth/death processes resp. the intensity of the dispersal flow between habitat patches. The local demography is affected by patch size, habitat quality (including heterogeneity) and nest predation (among other factors not discussed), the dispersal flow is related to the landscape structure.

for which fragmentation implies insularization of habitat.

Each fragment or habitat remnant may contain a population of a particular species, but local extinctions may cause vacancies. This is especially true for very small remnants, where populations may go extinct purely by stochastic demographic processes (Leigh 1981). A set of populations distributed over a number of habitat fragments is called a **metapopulation** as long as the subunits (subpopulations) are interconnected by dispersing individuals. Levins (1970) used the concept for 'a population of populations which go extinct locally and recolonize'. The metapopulation is the demographical unit at the landscape level; its degree of organization is of a higher order compared to that of the subpopulations in the fragments. The metapopulation dynamics are the result of the combined dynamics of the subpopulations and the between-fragment dispersal flow. Although Levins was the first to use the concept of metapopulation, Andrewartha and Birch in 1954 had stressed the spatial relations between 'local populations'. In population genetics 'deme' is an analogous concept. Recently, the con-

cept is being rediscovered (Harrison *et al.* 1988; Hastings and Wolin 1989; Hanski 1989) and applied in landscape ecology (Opdam 1987, 1988, 1990a,b; Merriam 1988) and conservation biology (Simberloff 1988; Bukey 1989).

The driving forces of metapopulation dynamics are local extinctions and recolonizations of vacant patches (Fig. 1). Local extinctions may be the outcome of birth and death processes in the subpopulations, partly determined by local habitat quality and fluctuations, partly by other types of local disturbance such as nest predation or nest parasitism (affecting reproduction). Particularly in small populations, the result of interacting birth and death processes can be described in terms of stochastic extinction. The relationships between the rates of local extinction and recolonization determine the mean longevity of subpopulations and, by consequence, the survival time of the metapopulation. Frequent local extinctions and recolonizations cause a distribution pattern to be dynamic: the species' distribution over the landscape shifts from year to year. This pattern can be simulated purely by assuming stochastic demographic processes in

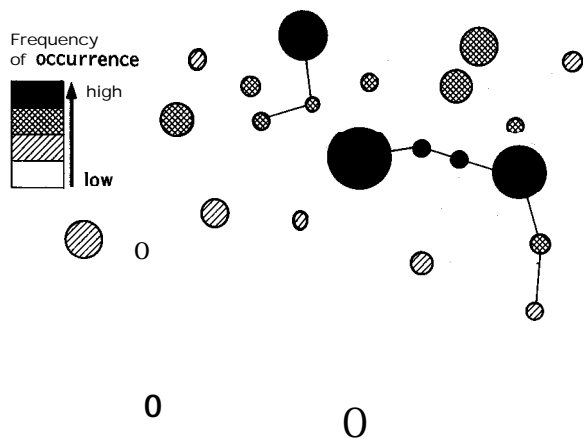


Fig. 2. Expected pattern of probability of occurrence in habitat fragments differing in size and isolation, for a species with a recolonization rate too small to compensate for local extinction immediately.

simplified 'landscapes' where all patches are equal and equidistant (Verboom, unpubl. results). In real-world landscapes, differences in patch size and interpatch distance will cause variation in extinction rate and in recolonization rate among the patches. On average, larger patches will be occupied more often and over longer continuous periods than smaller patches, whereas isolated patches will remain empty for longer periods than patches close to others (Fig. 2). A large area of habitat, containing populations being large enough to stay out of risk of extinction due to demographic stochasticity, and being a source of dispersers, may function as a stable distribution centre. Two extreme cases are depicted in Fig. 3.

Metapopulations may be delineated on the basis of (abrupt) changes in the landscape structure, particularly in average patch size and interpatch distance. Also, metapopulations can be delineated on the basis of the rates of the basic processes, but this will be less convenient. Generally speaking, we encounter similar problems as in drawing borderlines around populations and communities. In this review, a group of sample sites of a study is simply regarded as the framework for a metapopulation.

Birds are mobile animals. Many species migrate over short or long distances. This has led several authors (e.g. Ambuel and Temple 1983) to assume that the effect of isolation could easily be neglected

at a landscape level. However, there is a fundamental difference in proximate and ultimate factors between migration between summer and winter resorts and the unidirectional movements of (mostly immature) birds on their way from the site of birth to a subsequent breeding territory. There is much evidence that many bird species breed at distances on the order of several kilometers from the site of birth or former breeding place. This holds for resident species as well as for migratory species (Greenwood and Harvey 1982; Gauthreaux 1982). Therefore, possible effects of landscape structure must not be denied *a priori*.

The effects of fragmentation will be reviewed in two sections:

- Long-term studies of patch dynamics: have extinctions and recolonizations been observed?
- Short-term studies of distribution patterns: do distribution patterns match expectations from metapopulation theory?

Usually, I take presence/absence of single species, or its summation for a selection of species (e.g. the number of forest-interior species present in a breeding season) as a bird variable. Most studies in the literature have focussed on the number of species. I do not use it here as a community parameter, but simply as the overall result of the probabilities of being present for the individual species. Density is much more difficult to interpret because it is heavily influenced by environmental fluctuations within and outside the breeding area. In addition, the effects of isolation on density are ambiguous. Isolation may prevent emigration out of productive habitat types, causing extremely high densities, but it may also prevent replenishment of weak populations in poor habitat types.

### 3. Long term studies of metapopulation dynamics

Do fragmented bird populations show metapopulation characteristics? Do local extinctions and recolonizations occur?

Diamond (1984) argued that 1–30% of the bird species in oceanic islands and tropical forest fragments disappeared from one year to another. Also, Fritz (1979) could assess local extinctions and recol-

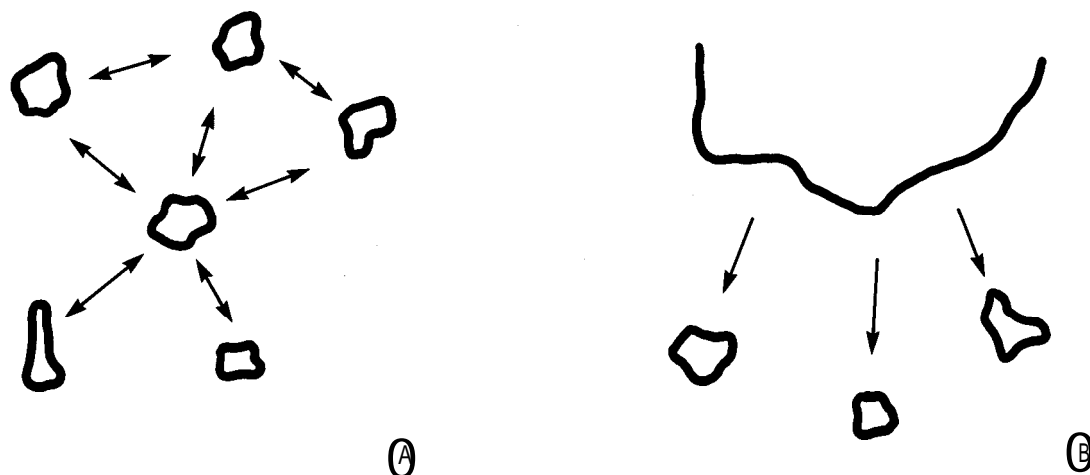


Fig. 3. Two examples of relationships among habitat patches in a fragmented landscape. A. All patches are about equal in size and all may become empty due to local extinction; patches are interdependent. B. A large patch serves as a continuous source of dispersers, supporting subpopulations in small patches and, hence, lowering local extinction chance there. Extinction rate in the large patch is assumed to be negligibly small.

onizations in the spruce grouse *Canachites canadensis*, and the same phenomenon was established for forest song birds in a 3-year study in The Netherlands (Van Noorden 1986). However, such turnover may also occur in equally sized sample plots with large forests. Observing such metapopulation dynamics is less relevant to the fragmentation problem than determining how landscape structure influences spatial dynamics. Therefore, extinction and recolonization frequencies in habitat fragments must be related to the size of these fragments as well as to the density of patches in the surrounding landscape and the density of putative dispersal corridors.

Van Noorden (1986) analysed census data for forest-interior species over 3 years from two agricultural landscapes with scattered forest fragments (ranging in size between 0.5 and 30 ha). He found a negative exponential relationship between frequency of extinction and woodlot area. Broadly speaking, this observation implies that the chance of going extinct increases rapidly below a local population size of about five breeding pairs. In a regression analysis, 47% of the variation in extinction frequency was explained by woodlot area; no habitat or isolation variable added to this simple model improved the model performance.

The European nuthatch *Sitta europaea* is a strictly sedentary species of mature deciduous wood-

land. Verboom et al. (unpubl. ms.) analysed three time-series of presence-absence data, encompassing a total of 128 small woodlots. Overall, 23 local extinctions were recorded. The extinction rate could be related to carrying capacity (maximal size of subpopulation), habitat quality, and a parameter for yearly variation.

These results confirm the observations from longitudinal studies of island avifaunas: local extinction probability is exponentially related to the area of the habitat fragment (cf. Diamond 1984), which is proportional to the size of the local population. This conclusion does not exclude other factors, however. For instance, environmental variability can cause populations to fluctuate and contribute to extinction rates, with species with different life histories affected differently. For birds in temperate zones, the effect of this factor on local population extinction has not been shown. Karr (1982), analysing data of 38 bird species on islands in the Panama canal, found that presence/absence of species was better explained by the amplitude of population fluctuations than by local population size, suggesting that environmental stochasticity had more impact than demographic stochasticity.

The chance that a year without a species being present is followed by a recolonization will depend on the degree of isolation of a patch. For birds, isolation can be expressed in terms of area of habitat

**Table 1.** Results of a multiple regression analysis on the frequency of immigration by forest-interior species into 74 mature **woodlots** in two agricultural landscapes in The Netherlands. Two area variables, 8 habitat variables and 10 isolation variables were considered. Isolation measures included distance to wood larger than 20 ha, amount of various types of woodland in surroundings and density of corridors. The immigration measure used was the number of species having colonized the **woodlots** between two consecutive breeding seasons, expressed as the proportion of all potential colonization (after Van Noorden 1986).

	Sign of coefficient	% variation accounted for
Study area <sup>1</sup>	-	15.5
Area of woodland within a 1 km distance	+	8.3
Area of woodland within a 3 km distance	+	4.1
Standard deviation of trunk perimeter <sup>2</sup>	+	5.2

<sup>1</sup> This parameter indicates that in one of the study areas recolonization chance was lower, either due to a smaller dispersal flow or a higher degree of isolation. The second option was not supported by differences in the isolation variables.

<sup>2</sup> This parameter can be interpreted as an indicator for habitat quality.

within a particular radius from the site of observation on related measures, like the mean distance to the nearest five patches or the distance to the closest patch exceeding a certain size (assuming this larger patch to be a constant source of dispersers). Another component of isolation is the density of possible corridors. Long-term studies comparing the immigration frequency between habitat patches in different landscape types are virtually lacking. The study by Van Noorden (1986) covered only 3 years; here, multiple regression model explained no more than 33% of the variation in the occurrence of recolonizations, of which 12% was accounted for by the area of woodland in the surrounding landscape (Table 1). Recently, Verboom et al. (unpubl. ms.) found the recolonization rate of nuthatches to be correlated with the average distance to other occupied patches.

#### 4. Short-term studies of distribution patterns

Most studies on fragmentation effects are short-term investigations, in which the probability of occurrence of a species (or the variation in the total species number, in which all species-specific probability values are combined) is correlated with one or several spatial features of the landscape and the individual patches. Species will more likely be present

the larger the patch and the higher the connectivity with other patches (Fig. 2). The advantage of a spatial correlation approach is that sample size can be larger than in longitudinal studies, so that the relationship between the probability of occurrence and the landscape structure can be quantified satisfactorily. However, to apply this relation in landscape planning, one has to assume that the year of the investigation is representative for any other year (which is not very plausible), that the correlation reflect causal ecological relations, and that the observed distribution is in equilibrium with the degree of fragmentation. The equilibrium assumption requires a steady state in the landscape pattern over a period long enough for the metapopulation to respond. For relatively shortlived species the response could easily take on the order of several decades. To my knowledge, nobody has ever estimated that period, and for this review I have to neglect the effect of this time-lag in the observed distribution patterns. However, this time-lag effect may postpone the expected relation to landscape pattern rather than producing an unexpected distribution.

In the following discussion, I only refer to studies in which isolation was explicitly measured. A number of studies infer a possible role of isolation from the z-coefficient in the logarithmically transformed species-area curve. This is only reliable under strict

Table 2. Details on the type of variation investigated in studies on fragmentation effects using a 1-year correlation approach, in which both area and isolation were measured and the analysis was restricted to species for which the original habitat became fragmented (excluding edge species and mosaic species).

	sample size	number of habitat types	number of habitat variables	range in patch size (ha)	distance to large area (km)	area of habitat in surroundings <sup>†</sup>	corridor density (number of variables)
Howe '84	12 + 12	1	6	0.1-7	0.5	—	—
Lynch <i>et al.</i> '84	183	6	7	2-1100	0.1-3	—	—
Opdam <i>et al.</i> '85	68	1	4	0.3-30	0.1-7	6(1,3 km)	3
Brown and Dinsmore '86	30	1	1	0.2-182	?	9(1,3,5 km)	—
Blake and Karr '87	14	2	28	2-600	?	—	—
Askins <i>et al.</i> '87	46		11	1-3000	—	2(2 km)	—
Van Dorp and Opdam '87	234	1	12	0.1-39	0.0-1.1	4	2
Soulé <i>et al.</i> '88	37	—	—	0.1-76	0.4-3	—	—

<sup>†</sup> Indicated is the number of variables measured, between brackets the length of the radius of the circular zone around the patch considered.

conditions (Martin 1981), and I decided to omit these studies (Sillen and Solbreck 1977; Moore and Hooper 1975; Kitchener *et al.* 1980; Murphy and Wilcox 1986) from this review.

Forman *et al.* (1976), Ambuel and Temple (1983), Hayden *et al.* (1985), Freemark and Merriam (1986), Anselin and Meire (1986) and Dickman (1987) did not regard isolation or *a priori* assumed it to be of negligible significance to birds. In the study by Whitcomb *et al.* (1981), patch area and isolation are highly correlated, so that their respective effects can not be disentangled. These studies are excluded also.

Also excluded are the studies in which all species are treated as being ecologically similar with regard to fragmentation. Examples of such studies are Helliwell (1976), Cieślak (1985), Vizyová (1985), Gotfryd and Hansell (1986), Ford (1987) and Decamps *et al.* (1987). In these investigations, the total species number is used as the only bird parameter, including patch-interior species, edge species, and species feeding in the adjacent matrix or even in the surrounding landscape mosaic. Only the patch-interior species can be expected to be negatively affected by fragmentation. Contrarily, fragmentation implies an increase in edge length and creates new habitat for mosaic species, resulting in an increase of these species. Van Dorp and Opdam (1987) found a significant role of isolation when only forest-interior birds were regarded, whereas

no effect was found for the total of forest-interior and edge species combined. What is left to discuss here is a group of papers treating the variation in the number of a selection of species or the density of ecological groups in a multiple regression approach, using a variety of definitions of area, habitat, and isolation as independent variables (Lynch and Whigham 1984; Howe 1984; Opdam *et al.* 1984, 1985; Brown and Dinsmore 1986; Askins *et al.* 1987; Blake and Karr 1987; Van Dorp and Opdam 1987; Soulé *et al.* 1988). The sample of observed patches ranges between 14 and 235 and the range of patch size varies from 0.1 to 3000 ha (Table 2). Some studies treat species separately, which also holds for single-species studies by Fritz (1979), Müller (1982) and Petterson (1985).

#### 4.1. Woodland habitats

The sample taken by Lynch and Whigham (1984) covered a broad array of forest habitat, which is reflected in the dominant role of habitat variation in explaining distribution patterns. Contrarily, Van Dorp and Opdam (1987) found habitat variation to account for only 2% of the variation. This undoubtedly is a consequence of their way of sampling, in which they kept habitat variation among patches as small as possible. The same can be said about Howe's (1984) study. These examples illus-

trate a very obvious, but sometimes forgotten, drawback of regression approaches: the variation included in the sample determines the contribution of factors relative to the total variation accounted for. This must be kept in mind in the following.

All investigations demonstrate an effect of area and, with the exception of the Blake and Karr (1987) study (encompassing a very small sample size), an effect of some isolation component. The relative contribution of area and isolation is difficult to assess, due to the variation in ranges (Table 2), the differences in scale, and the partial correlations in some of the studies. Roughly speaking, it seems that the role of area greatly exceeds that of isolation over distances in the order of magnitude of several kilometers.

Usually, isolation is expressed as the total amount of habitat within a circle around the site of observation, or as the shortest distance to a larger area that might function as a permanent source of dispersers. A possible role of linear landscape elements as dispersal corridors was investigated only by Van Dorp and Opdam (1987). Where several isolation factors were included in the study, these could often be used as alternatives in regression models (Opdam *et al.* 1985; Van Dorp and Opdam 1987; Askins *et al.* 1987).

Howe (1984) followed a different approach. He compared a small number of **woodlots** with equally sized samples taken from a large forest. The **woodlots** supported higher densities, but rare forest species were often lacking. After accounting for area effects, isolation variables contributed significantly to a multiple regression on number of forest species.

Soulé *et al.* (1988) compared the bird faunas of patches of chaparral scrubland that became fragmented during the extension of the city of San Diego, California, and they also regarded the duration of the period in isolation. Typical chaparral species have a higher probability of being absent from isolated patches; the smaller the patch size and the longer they have been isolated. None of the isolation variables showed significant correlations, which was interpreted as an indication that fragmentation-prone species are not capable of crossing 50–100 m wide barriers of buildings and roads, (at least within the time scale of the study), indicating

that virtually all patches were equally isolated.

A general conclusion from these studies on woodland birds is that isolation, measured at landscape scale, can be a significant factor to birds. However, in regression, the size of habitat fragments always explains a much larger part of the variance in the bird parameter. The relative importance of these two components of fragmentation seems to be scale-dependent, and will also depend on the dispersal capacity of the species concerned.

#### 4.2. Marshland habitat

In general, species of stable, predictable types of habitat are expected to be more site-tenacious and to disperse over shorter distances than species of unpredictable habitat types. Hence, forest-interior species might follow a strategy of settling near the place of birth and stay there for the remainder of their breeding seasons (although in the meantime most species migrate over considerable distances!). Contrarily, species of marshland may tend to disperse over larger areas, being capable of responding to sudden changes in the distribution and quality of their habitat. If so, one would expect marshland birds to show isolation effects at a more regional scale than forest birds do.

Reichholf (1984) claimed to have evidence for a critical distance on the order of 100 km between marshland areas to conserve bird species in isolated marshes. However, any distance of this kind will vary with the quality of habitat and of the size of the isolates (being the key factors driving local extinction and the dispersal flow), and Reichholf did not support his conclusion with information on these factors. The investigations of Brown and Dinsmore (1986) revealed a convincing influence of isolation on marshland avifaunas. Their regression model contained only size and area of marshland within a 5-km radius and explained 75% of the variation in species number. Ten out of 25 species did not occur in marshes smaller than 5 ha. Contrarily to my expectation, this suggests that marshland species are affected by isolation at the same spatial scale as forest-interior birds are.



### 4.3. Single-species analyses

Comparisons at the species level may yield more insight into features that make species susceptible to fragmentation. Except for problems in finding sufficiently large samples at similar spatial scales, there is a need for much larger sample sizes than in studies focussing on species number. Species number can be analysed with regression assuming normal distribution of variables, but presence/absence patterns of single species can only be treated by logistic regression techniques, because a poisson distribution has to be assumed. This technique is less powerful in detecting significant correlations, and the only solution to that problem is to enlarge sample size.

A nice example of a study focussing on a single species is Müller's (1982) analysis of the distribution pattern of the middle spotted woodpecker *Dendrocopos medius* in oak forest remnants in central Switzerland. Müller censused 99 woods ranging in size between 3 and 165 ha and situated at distances up to about 10 km from the next oak wood larger than 40 ha. A combination of these two variables explained a good deal of the difference in presence/absence among the woodlots. The species was always absent from woodlots at more than 9 km distance from the larger oak wood. Later, the susceptibility of this woodpecker species to fragmentation was confirmed by Petterson (1985), who documented the total extinction of the last meta-population in southern Sweden.

For the spruce grouse *Canachitis canadensis* in North America, Fritz (1979) published data showing that it was lacking most frequently in the most remote habitat patches (more than 10 km from the nearest patch).

Some of the authors who analysed species number selected a sample size large enough to permit analysis for single species. Van Dorp and Opdam (1987) presented data for 32 woodland species. Among these species, 26 showed significant effects of area, 16 were affected by isolation at a regional geographical scale (over a distance of roughly 100 km), and 11 were found to correlate with distance measures at the landscape level. Species restricted to mature deciduous forest (which was relatively

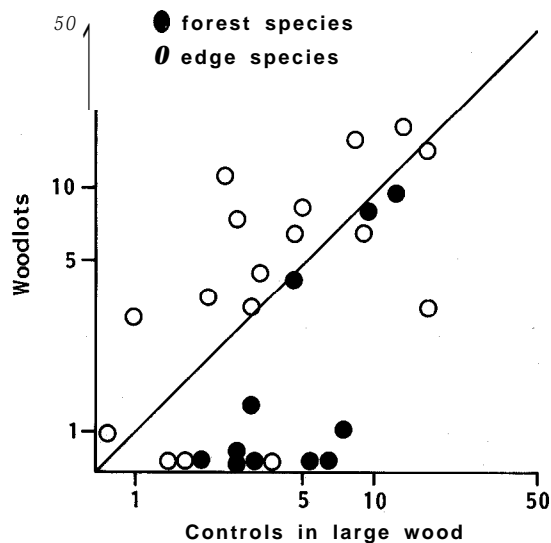


Fig. 4. Comparison between the density of bird species in woodlots and the density in equally sized plots in a large nearby forest. Most forest species are scarcer in woodlots than expected on the basis of control plots (based on Howe 1984).

scarce in the area of study) showed the strongest effects of isolation, e.g. the nuthatch *Sitta europaea* and the marsh tit *Parus palustris*.

In North America, Howe (1984) and Lynch and Whigham (1984) offered data that permitted more insight into the susceptibility of individual species to fragmentation. Howe's results from Wisconsin nicely demonstrate the underrepresentation of forest-interior species in woodlots compared to similar-sized plots in large forests, whereas edge species are usually more common in woodlots (Fig. 4). Of the species on which Howe offered details, 17 are also included in a table of results of regression analysis in Lynch and Whigham's paper. Thirteen are similar as to whether they are affected by fragmentation or not, whereas the remaining four species show inconsistent results. A problem with such a comparison is that regional abundance levels may differ considerably between Wisconsin and Maryland. A species abundant in one region may show weak effects of fragmentation at a given spatial scale, whereas in another region where it is less abundant, it may be found to be influenced by patch size (as was demonstrated by Van Dorp and Opdam 1987). Investigations on a larger geographical scale must always consider the possible varia-

tion among parts of the investigated area, and add it as a variable to a regression analysis.

## 5. Discussion

### 5.1. *Fragmented forest bird populations as metapopulations*

Metapopulation theory is helpful in understanding the effects of fragmentation on a species. The theory stresses the spatial stochasticity of a species' distribution over a fragmented landscape, caused by local extinctions and **recolonizations**. Through time, a spatially dynamic distribution is observed as a shifting pattern of occupied and empty patches. In a single year a patch may be found empty for no obvious reason other than demographically stochastic events. Patches differ in the probability of being occupied as a result of different spatial characteristics: patch size, habitat quality, distance to other patches, and resistance of the landscape matrix.

In fragmented agricultural landscapes under heavy human pressure, the size and quality of patches tend to decrease and landscape resistance tends to increase (e.g. elimination of hedgerows), causing the balance between the rates of extinction and recolonization to shift to a point where, on average, a smaller number of patches is occupied. As the proportion of empty patches increases, the survival probability of the species in the landscape will decrease. Thus, the metapopulation approach links long-term processes of spatial dynamics and survival to spatial landscape characteristics.

Also, the metapopulation concept teaches us that, as long as a subpopulation forms parts of a network of interacting subpopulations, it makes no sense to isolate a reserve or landscape patch and ask questions about minimal patch size or minimal viable population size. These concepts must be considered in the light of the dispersal flow and the resulting recolonization chance. Likewise, discussions about a rationale behind a choice between 'several small or single large reserves' must consider the dynamic character of a species' distribution over these reserves instead of reducing this problem to a single

deterministic summing up of species lists from a single year (or even worse: many different years).

Much evidence supports the predictions, drawn from the metapopulation theory, that small local populations in landscape fragments go extinct and become reestablished through time. However, most of the evidence comes from single-year pattern studies showing species to be absent in what are assumed to be suitable pieces of habitat; the probability of being absent could be related to the size of the patch and to its isolated location. There is a serious paucity of long-term studies, in which (unlike those by Butcher *et al.* 1981 and Askins and Philbrick 1987) the presence/absence dynamics of a metapopulation is followed in a great number of landscape patches to assess extinction frequency and recolonization frequency and to relate these parameters to characteristics of the landscape.

There are at least three reasons for such an approach. First, the interpretation of correlation patterns is always overshadowed by the possibility of having put the wrong process to the observed pattern. Second, landscapes are often subject to change. In particular, the farmland landscapes in which many of the pattern studies were situated often became increasingly fragmented over the last decades. A change in landscape structure is followed by a change in the mean extinction and/or the recolonization rates for the metapopulation, but it might take many years before a new dynamic equilibrium with a new average probability of being present will be adjusted. An ecologist measuring one year in the course of this relaxation process may get an optimistic impression of a species adaptability to fragmentation of its habitat.

The third reason for long-term studies at a landscape-wide scale is the need for calibrating and testing metapopulation models. Models are the only scientific tool to extrapolate into the future and make predictions about the longevity of **metapopulations** and the impact of fragmentation on the survival chance of a species in a landscape. Such models necessarily are stochastic, since local extinction in a small population must be considered as a demographically stochastic process. Consequently, the development of such models as well as the adjustment with field data will be an enormous

challenge to (landscape) ecologists, but will be an indispensable basis for application in landscape management and planning. Urban and Shugart (1986) made an interesting first step in simulating avian metapopulations. Their model produced relationships of area and isolation to population persistence that are in accord with empirical evidence. Verboom *et al.* (unpubl. ms.) developed a stochastic metapopulation model for the European nuthatch *Sitta europaea* that is also consistent with observations of patch dynamics.

### 5.2. Dispersal movements through a fragmented landscape

Dispersal is rarely observed and therefore hard to measure. A serious paucity in our knowledge of forest birds' reactions to fragmentation is how dispersers move through the landscape. Are they really reluctant to cross open fields and, if so, over what distances? Do hedgerows or small clumps of trees decrease the resistance of the landscape to natal dispersers, and do highways or urban areas act as barriers? We need answers to such questions to be able to understand better the effects of fragmentation observed at the metapopulation level. We also need them for application of our knowledge in landscape planning, for example with regard to questions about the need to construct corridors. Also, distribution statistics of dispersal distances are indispensable for studies with mathematical models.

However, most studies of dispersal have been based on movements of banded individuals over a mixture of landscape types. A general observation seems to be that the distribution of dispersal distances resembles an exponential or skewed normal function: most individuals cover short distances, a few are found at remote sites (e.g. **Delius** 1965; Berndt and Sternberg 1968; Greenwood and Harvey 1976; Eden 1987; Enoksson 1987; Matthysen and Schmidt 1987). I am not familiar with studies concerned with the relation between landscape structure and dispersal pattern, except for the study on nuthatches by Matthysen and Schmidt (1987). They compared the proportion of ringed nestlings reco-

vered in the area of birth between isolated woods and continuous woodland, but found no difference. Studies of this kind are badly needed.

### 5.2. Effects of nest predation and nest-parasitism on local extinction

Predators and parasites have been reported to affect breeding efforts of forest birds in **woodlots** or in wood edges. This factor could lower the local reproductivity of subpopulations, and hence increase local extinction rate. Do we have evidence for such an effect?

Several studies (Gates and Gysel 1978; Brittingham and Temple 1983; Andren *et al.* 1985; Wilcove 1985; Wilcove *et al.* 1986; Small and Hunter 1988; **Andren** and Angelstam 1988) claimed that the reproductive output of song birds in small **woodlots** can be smaller than in large ones due to nest predators and nest parasites. Some of them argue that fragmentation would result in the disappearance of top predators, causing an increase in the density of predators of a lower level, like crows, squirrels, and raccoons. However, the assumption that top predators would restrict the density of second-order predators is not empirically supported, and systematic census data from fragmented and non-fragmented landscapes are not given. An exception is the study of Andren *et al.* (1985), showing that predation in experimental ground nests, both in grassland and in woods, increased with a decreasing proportion of woodland, possibly due to an increase in corvid species. Wilcove (1985) compared predation levels in **woodlots** in suburban and rural landscapes. In the suburban **woodlots** (4-12 ha), 71% of artificial nests containing quail eggs were found by predators, whereas in rural **woodlots** this proportion was 48%. These small and two large (283 and 905 ha) rural **woodlots** did not differ in predation pressure.

In other studies (Gates and Gysel 1978; Brittingham and Temple 1983; Wilcove *et al.* 1986; Andren and Angelstam 1988; Small and Hunter 1988) nest losses due to predation and parasitism were relatively high in edges of forest or in small woods as compared to large ones, suggesting that predators and parasites associated with agricultural land-

**scapes** intrude into the forest edge from outside. This effect was found over a large variety of distances, ranging from tens of meters to 600 m. This variation could be related to the structure of the forest vegetation, the type of the surrounding landscape, and biogeographic differences in the predator fauna, but it could also vary between years due to density fluctuations in predators or alternative prey.

Of course, assessing a decrease in predation pressure from the edge of a habitat fragment to the interior does not necessarily imply a lowering of reproductive rate, let alone an increase in local extinction rate. Many bird species can lay several replacement clutches, and there are some other mechanisms in the population dynamics of a species as well to compensate for lower reproduction, such as reduction in immature or adult mortality.

### 5.3. Some questions for future research

Virtually all studies of fragmentation effects on birds were carried out in agricultural landscapes with scattered woods in Europe and North America. This may cause a serious bias in generalizations of fragmentation effects. It may be that in such landscapes fragmented populations show characteristics of metapopulations, but it does not imply that this is also the case in naturally fragmented populations, where the spatial scale of the landscape pattern can be very different. There is a great need for studies in such landscapes. Also, it is not self-evident that other **taxa** will show **metapopulation** behaviour in fragmented agricultural landscapes. Much depends on the interplay between spatial scale and species characteristics, like average subpopulation size and fluctuations relative to the average patch size, and to the capability of the species to cross barriers and gaps (Opdam 1990b).

There is also a considerable bias towards woodland biota. Since site tenacity and dispersal capacity are expected to be related to the predictability of habitat suitability over time, fragmentation effects in avian communities of woods should be compared to those in less predictable and more changeable habitat types.

A third point is about the genetical adaptability of species to fragmentation. For instance, do species develop a tendency to disperse over longer distances as fragmentation of habitat increases? To my knowledge, this question has never been **considered**.

Finally, we will have to link the landscape level to the biogeographical level of scale. In their turn, metapopulations form part of a larger spatial system, the distribution area of a species. Since the species' range changes over time, metapopulations may die out and **(re)appear** as a result of processes on a larger spatial scale. Hengeveld (1990) showed that this is particularly true at the border of the distribution range. He also argued that, in this border zone, species tend to have lower reproductive success and poorer dispersal capacities (or, broadly speaking, have lower ecological fitness). This suggestion is an interesting basis to compare the functioning of bird metapopulations in fragmented landscapes with similar spatial dimensions, but in various locations within the species range.

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