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Deciduous forest and resident birds: the problem of fragmentation within a coniferous forest landscape

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Abstract

Six species of resident birds were censused in patches of deciduous forest within a coniferous forest landscape in south central Sweden. Here, the forests have been subjected to active forestry for a long time, but with recently increased intensity. Although the forest cover is more or less continuous in this landscape, mature deciduous forest is now a rare element compared with the untouched forest.

All censused patches were similar with regards to size, proportion and amount of deciduous trees, but were either isolated in the coniferous forest ('isolated patches') or near to other deciduous patches ('aggregated patches'). We concentrated on six species of resident birds, with moderate area requirements, that are tied to deciduous forest and whose ecology is well-known. The Nuthatch and the Marsh tit, which both show strict year-round territoriality and have a restricted dispersal phase, were significantly more likely to be found in aggregated than in isolated patches. No effect was found for the Great tit and the Blue tit, which are less territorial outside the breeding season and have a longer dispersal phase. Moreover, the Great tit is less specialized on deciduous forest than the other species. Also, the Long-tailed tit was negatively affected by isolation, which may be due to restricted dispersal and to larger area requirements of this flock-territorial species. The Hazel grouse, finally, was not affected, but this larger bird probably uses the forest in a different way from the smaller species.

Our study clearly shows that fragmentation of one type of forest (deciduous) within another can have serious detrimental effects on forest-living species and raises important issues for forest management practices and conservation within a forest landscape.

Introduction

Fragmentation of continuous forests is a problem that has been addressed in several studies (e.g. Blake and Karr **1987,** van Dorp and Opdam **1987,** Laurance **1990,** Wilcove and Robinson **1990,** Blake **1991,** Saunders ***et al.* 1991).** However, two important restrictions apply to many studies, viz., **1)** These studies have usually been performed in three-dimensional patches (e.g. forest) in a two-dimensional matrix (such as fields or water) and 2) taxonomically rather than ecologically coherent groups have often been studied. Important patterns may be masked by such rather broad approaches (cf. Opdam ***et al.* 1985).**

Fragmentation need not always involve such dis-

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tinctly different habitats as e.g. forest and arable land, but may also occur ***within*** a forest, if one type of forest habitat becomes fragmented within another. Furthermore, to understand the processes by which species are lost when natural landscapes become altered or fragmented, we must relate landscape changes to the biology of the species. For example, most studies of effects of forest fragmentation on birds have treated migrant and resident species as equal, although several studies clearly show that these two groups may react differently to landscape changes (Vaisanen ***et al.*** 1986, Angelstam 1991). Habitat requirements for year-round residency are likely to differ from those of presence merely during the breeding season. Habitat qualities like food density, nest (roost) holes etc. are as important during winter as during the breeding season. In a seasonal environment, such as temperate forests, many resident species are resource limited during autumn/winter (e.g. Enoksson 1990), while roosting holes can reduce temperature loss during night (Kendeigh 1961, Askins 1981). Thus habitat changes, such as fragmentation may have quite different effects on resident species than on migrants. However, neither these two groups are uniform, but different resident (as well as migrant) species may react differently. Still, this division is a useful starting point.

Modern industrialized forestry involves dramatic changes to forests, which affect the species that reside there. For resident birds of the boreal forest, the most striking effect of modern practices, apart from the reduction of older forests themselves (Helle and Jarvinen 1986), is the severe reduction of the deciduous component in middle-aged and old taiga forests (Angelstam 1990, 1992, Swenson and Angelstam 1993). In most cases only small and distinct patches remain, which in a coniferous landscape can be seen as islands to species restricted to the deciduous forest. Size, isolation and the surrounding matrix then become important factors influencing the likelihood that such species can persist in the forest (cf. Saunders ***et al.*** 1991). Characteristics of the individual species, such as dispersal ability, area requirements and degree of habitat specialization will determine which species are affected and how.

In this paper we examine whether resident bird species specializing on the deciduous component in taiga forests are affected when their habitat becomes isolated. We concentrate on the effect of isolation, keeping the size of fragments as well as the character of the surrounding matrix constant. Thus, we examine a possible effect of fragmentation when one type of forest (deciduous) is fragmented within another (coniferous), that is, fragmentation on a less obvious scale than in many other studies. We also try to relate differences in response between species to differences in their ecology, especially dispersal behaviour and habitat specialization.

Methods

Study area

The study was performed around Grimsö Wildlife Research Station (59°45′N, 15°30′E) in the Bergslagen area, south central Sweden. Here, the landscape consists of a continuous and almost homogeneous coniferous forest containing very little deciduous forest, as well as some agricultural land, mires and lakes. The deciduous patches used in this study are associated with old abandoned pastures, which today have a canopy of birches ***Betula pubescens*** and ***B. verrucosa,*** aspen *Populus tremula,* alder *Alnus* spp. and Norway spruce ***Picea abies*** and an understory of mixed young coniferous and deciduous trees. The surrounding forests are totally dominated by Norway spruce and Scots pine ***Pinus sylvestris***.

Compared with other boreal forest landscapes, Swedish forests have been exploited and managed for a very long time. Man had started to use forests intensively already by the 16th century, mainly for charcoal production. The present forest landscape is shaped and dominated by modern forestry. Compared with the natural forests, the conditions for fauna and flora are highly altered. For example, the dominant disturbance in the natural forest, uninfluenced by humans, was fire, which produced a landscape with high structural, temporal, and spatial variation (Angelstam in press a, b). After a fire, succession started with deciduous trees such as birches and aspen and ended with the conifers,

Table 1. Amount of deciduous and deciduous + mixed forest, respectively, within a 1, 2, 3 and 4 km radii of aggregated and isolated (see text) study patches. Mann-Whitney U-test, 1-tailed, corrected for ties.

		Mean amount of deciduous forest (ha) within			
		1 km	2 km	3 km	4 km
Aggregated patches	n = 15	18	63	120	230*
Isolated patches	n = 15	8	15	30	63
	p =	0.0023	0.0001	0.0001	0.0021
		Mean amount of dec. + mixed forest (ha) within			
		1 km	2 km	3 km	4 km
Aggregated patches	n = 15	36	128	243	444*
Isolated patches	n = 15	13	32	60	127
	p =	0.0002	0.0001	0.0001	0.0008

* n = 13 as two patches were situated less than 4 km, but more than 3 km, from the border of the mapped area; consequently, the amount of deciduous forests could not be measured for that interval.

spruce and pine. Standing and down dead wood was abundant. In comparison, present day forest patches are large and structurally simple. Logging is followed by site preparation, plantation, precommercial thinning and finally logging again. This has resulted in a maximization of the wood resource aspect of the forest system at the expense of biodiversity and natural processes (Ingelog *et al.* 1991, Esseen *et al.* 1992, Angelstam 1992). In contrast to the succession in a natural forest, there is no successional stage with older deciduous trees. At present, mature deciduous trees are only found near lakes, streams, abandoned pastures etc. Indirect effects of the alteration of the forest landscape, such as high browsing pressure on deciduous trees/shrubs due to high densities of herbivores, further reduces biodiversity (Angelstam 1990).

Thus, the present-day forest is totally different from the natural taiga forest it has replaced. Its dynamics differ from that of primeval forest in several ways, both structurally within a patch and with regards to disturbance frequency and pattern within the whole landscape (van Wagner 1978, Harris 1984, Hunter 1990, Esseen *et al.* 1992, Angelstam 1992, in press a, b). The most dramatic changes have taken place since the late 1950s, that is during the last 2% of the time that taiga forest has been present here.

Selection of deciduous forest patches

Within a study area of 1000km^2, we selected deciduous patches with the aid of maps prepared by the Department of Physical Geography, Stockholm University, Stockholm (Ihse and Lovgren unpubl.). These maps were based on aerial infrared photographs (Ihse 1993). In these photographs, deciduous forest stands out in bright red. Thus, we were able to get a good and clear overview of presence and distribution of the deciduous patches within the coniferous forest. With this method, deciduous patches as small as 0.25 ha may be distinguished. All patches included in our study consisted of mature (> 70 years) trees.

In general, the deciduous patches are rather aggregated in their distribution within this coniferous forest. Thus, several patches may occur quite close together, while a few others have become isolated, with no other deciduous patch in the vicinity. Thirty deciduous forest patches were selected for study. Fifteen patches, that were surrounded almost solely by coniferous forest with very few other deciduous patches within a 4 km radii, were defined as 'isolated'. Another fifteen patches were defined as 'aggregated' in the forest, situated in or very close to an area with aggregations of deciduous patches. Mean distances from a study patch to the nearest patch of deciduous forest was 363m and 1.413m, aggregated and isolated stands, respectively. Median distance were 350m and 1250m, respectively. The amount of deciduous forest as well as of mixed forest within 1, 2, 3 and 4 km from a studied patch differed markedly between the two groups of forests, confirming our classification (Table 1).

The study patches ranged between 3–14 hectares. Due to the forest structure and the relatively small amount of deciduous forest, some variation in size could not be avoided, but most were close to

Table 2. Characteristics of aggregated and isolated patches. Student t-test, 2-tailed.

Property	Aggregated patches (n= 15)			Isolated patches (n= 15)			p =
	mean	s.d.	range	mean	s.d.	range	
Size (ha)	8.9	3.2	3–14	8.0	1.7	5–10	0.330
Canopy height (m)	20.2	3.0	14–26	18.7	2.1	15–23	0.116
% dec. trees	65.5	19.3	38–86	70.4	11.3	21–92	0.404
% dec. canopy cover	64.4	16.6	38–88	61.5	11.6	42–76	0.597

Table 3. Species presence in aggregated and isolated patches. X^2-test, 2-tailed.

Species	Aggregated patches (n = 15)	Isolated patches (n = 15)	p =
Nuthatch	7	2	0.046
Marsh tit	9	0	0.000
Long-tailed tit	7	1	0.013
Blue tit	9	8	0.712
Great tit	15	15	1.000
Hazel grouse	5	8	0.269

10 hectares. There were no differences in average size between the two categories of aggregated/isolated patches (Table 2). Neither did the patches differ with respect to canopy height or proportion of deciduous trees (Table 2).

Field procedure

We recorded presence and absence of resident birds in the selected patches during spring 1991. The seasonal song activities of resident bird species peak about one month before the peak in song activity of the numerically dominating sub-tropical and tropical migrants (mid-May–mid-June). This is of great practical importance, as residents can be censused before the arrival of migrants, that is, while the forest is still relatively quiet. Therefore, census of the residents was made from 9 April to 9 May 1991. Each patch was visited twice during this period; one early morning visit (5.00–8.00 a.m.) and one late morning visit (8.00–11.30 a.m.). Each visit lasted about three hours, during which time the observer walked slowly through the patch, taking care that no point in the patch was more than 50m away. This conforms to standard Swedish breeding bird census (Svensson 1975). A Hazel grouse ***Bonasa bonasia*** pipe was also used (Swenson 1991a).

We analysed presence of six resident species, that all are associated with deciduous forest. Nuthatch ***Sitta europaea,*** Long-tailed tit ***Aegithalos caudatus***, Marsh tit ***Paruspalustris,*** Blue tit ***P. caeruleus*** and Great tit ***P. major*** all are fairly small in size, have moderate demands on territory-size and have been found in woods smaller than ***5*** ha situated in agricultural land (Moore and Hooper 1975) or surrounded by water (Ahlén and Nilsson 1985), which suggests that the patches used in this study are large enough for the species in question. Furthermore, we included one **of** the larger species, the Hazel grouse. This bird is also territorial throughout the year and it has been suggested that it may be negatively affected by habitat fragmentation (Swenson 1991b, c).

Results

Effects of isolation

The Nuthatch, Marsh tit and Long-tailed tit were much less frequent in isolated patches than in aggregated, while no effect of isolation was found for the Blue tit, Great tit and Hazel grouse (Table **3).**

Effects of forest patch size

Variation in patch size did not affect the occurrence of the five smaller species. For example, even the

Table 4. Presence (+) vs. absence (–) of a species in a patch in relation to patch size. Student t-test, unpaired 2-tailed.

	Nuthatch		Marsh tit		Long-tailed tit		Blue tit		Great tit		Hazel grouse	
	+	–	+	–	+	–	+	–	+	–	+	–
Aggregated (n = 15)												
No of patches	7	8	9	6	7	8	9	6	15	0	5	10
Mean areas (ha)	9.3	8.6	8.7	9.3	8.7	9.1	8.6	9.5	8.9	–	10.6	8.1
p =	0.70		0.71		0.81		0.59		–		0.160	
Isolated (n = 15)												
No of patches	2	13	0	15	1	14	8	7	15	0	8	7
Mean area (ha)	8.5	7.9	–	8.0	9.0	7.9	7.9	8.1	8.0	–	8.6	7.3
p =	0.68		–		0.57		0.78		–		0.140	
Total (n = 30)												
No of patches	9	21	9	21	8	22	17	13	30	0	13	17
Mean area (ha)	9.1	8.2	8.7	8.4	8.7	8.4	8.2	8.8	8.5	–	9.4	7.8
p =	0.38		0.79		0.72		0.58		–		0.087	

smallest patch was found to contain both the Marsh tit and the Long-tailed tit. No differences were found when presence of these bird-species was tested against the size of the patches, neither between nor within the two groups (Table 4). There may be some indication though, that patch size was important for Hazel grouse (Table 4), although the difference in size between occupied and unoccupied patches (9.4 vs 7.8, respectively; Table 4) is certainly very small. However, this issue must be investigated further before any conclusions can be drawn.

Discussion

Deciduous forests patches as islands in the conger-ous forest

The theory of island biogeography (MacArthur and Wilson **1967)** has been used to explain the presence/absence of forest birds, not only on islands in lakes, but also in forests fragmented by agricultural land. Both the size and isolation of the 'islands' have a great effect on species diversity (Moore and Hooper **1975,** Ahlén and Nilsson **1982,** van Dorp and Opdam **1987).** However, to a forest bird, both true islands and woodlots in an open agricultural landscape are surrounded by a 'hostile' matrix. In this study, the deciduous patches were islands not in an open landscape, but in a forest. This may influence the effects of both size and isolation, as compared to studies performed in, for example agricultural landscapes. In a forest landscape, negative effects of small size might to some extent be compensated for, if the edge zone between deciduous and coniferous forests can be utilized to a greater extent or is less dangerous (e.g. does not have the increased predation pressure that is often found in edge zones; cf. Wilcove ***et al.*** **1986,** Andrén **1989)** than in the transition from forest to open land. Temple **(1986)** found size of fragment core area to be much more important than total fragment size in explaining the responses of forest birds to habitat fragmentation. It could well be that, to a forest bird, the core area of a deciduous patch surrounded by coniferous forest is more or less equal to the whole patch, while only the central part of a patch that is surrounded by open fields functions as core area. Thus, one might expect a species to be found in smaller fragments within a forest matrix than in an open one.

Furthermore, the coniferous forest matrix may provide more protection against predators than would open fields or water and should therefore be less deterring to a dispersing forest bird. Thus, isolation could be less important in this less hostile matrix. On the other hand, in many agricultural landscapes, the matrix is not uniform, but hedgerows, single trees and very small woodlots may

functions as corridors or stepping stones and facilitate the movements of animals and make species less susceptible to isolation (van Dorp & Opdam 1987, Potter 1990).

Nevertheless, also in forest landscapes, both patch size and isolation may influence the probability of the number of species found in a given patch. In our study, size of the deciduous patches studied did not explain variation in occurrence of species between patches, neither within the groups of aggregated and isolated patches nor in the two groups combined (Table 4). However, this does not mean that patch size is unimportant in this landscape, as we tried to minimize the effects of size in our study by chosing patches with as little variation as possible as well as of a size acceptable to the species we focused on. Other birds of the deciduous forest with larger area requirements are the Green woodpecker ***Picus viridus*** and the Lesser spotted woodpecker ***Dendrocopos minor.*** Only very few Green woodpeckers and no Lesser spotted woodpeckers were observed in this study (Enoksson ***et al.*** unpubl. data), suggesting that the size of the study patches were too small for these species, or that the ***total amount*** of deciduous forest is now too small in this landscape (cf. Angelstam and Mikusinski 1994).

In a study in an agricultural landscape in the Netherlands, van Dorp and Opdam (1987) found size to be the most important variable in explaining number of bird species present in different woodlots. However, as they studied the effects of size and isolation simultaneously, they had selected woodlots with a much larger variation in size than our study patches and furthermore, some of them were very small (0.1 ha). Our patches were, with one exception, between **5** and 15 ha in size. For woodlots between **5** and 10 ha in size, van Dorp and Opdam (1987) found a fairly high probability of occurrence **(>0.6)** of four of the six species included in the present study. The exceptions were Long-tailed tit, which attained this probability for woodlots larger than 10 ha, and Hazel grouse not at all present in the Netherlands. Isolation, on the other hand, was in the Dutch study as in our study (Table 3) found to influence the occurrence of Nuthatch, Marsh tit and Long-tailed tit, but not the Great and Blue tits. Thus, the results of two studies performed in different matrices still give very similar results.

Why are some species affected, but not others?

In this study we concentrated on six species of birds. They are all more or less resident, monogamous and territorial. Still, their response to the changes in the forest differed. There was a significant difference in occurrence of Nuthatch, Marsh tit and Long-tailed tit between aggregated and isolated patches, but neither Great or Blue tit, nor Hazel grouse were affected by isolation (Table 3). It is not simply that the distances are too far for some species to move but rather that they do not find the isolated patches. Also in an agricultural landscape, Opdam ***et al.*** (1984) concluded that distances of open ground restricted immigration rates of woodland birds far below the distance they are able to cover by flight. This may be even more true in a forest landscape, where a dispersing bird need only make many very short flights, but may have difficulties in actually locating small or isolated patches of good habitat.

During winter, when food-resources become scarcer and the temperatures are lower, access to food and protected roosting sites are very important for the survival of resident birds. Therefore, some species defend year round territories, either as a pair like the Nuthatch (Enoksson 1987, 1988) or a flock as in the Marsh tit (Nilsson and Smith 1988) and the Long-tailed tit (Gaston 1973). The ecology of both the Nuthatch and the Marsh tit has been well studied (e.g. Enoksson 1988, Matthysen 1988, Nilsson 1988). In both species, juveniles settle into these territories already in late summer and competition during this time has been suggested to result in restricted dispersal (e.g. Nilsson 1988). For the Nuthatch, natal dispersal distances are generally 1km or less and once juveniles have settled into these summer territories, very little movement occurs (Enoksson 1987, unpubl., Matthysen and Schmidt 1987). However, more important than actual distance moved, may be the very short time during which dispersal takes place (Matthysen 1987). Juveniles may thus be less likely to find iso-

lated habitat patches, when compared to species that do not settle definitely until spring, for example the Great and Blue tit.

Both Blue tits and Great tits join large winter flocks with other tit species and roam over an extended area during winter (van Balen and Hage **1989).** Especially during harsh weather, they may accumulate near houses and gardens, and part of the population migrates (Perrins **1979).** Thus, these species are much less likely to be affected by isolation within the distances used here, than the Nuthatch and the Marsh tit. Furthermore, the Great tit is not restricted to deciduous forests in the same sense as Nuthatches, Marsh, Long-tailed and Blue tits (Ulfstrand **1962, 1976).** Not surprisingly it was found in all the studied sites. Also the Blue tit was found equally in aggregated and isolated patches.

The Long-tailed tit is less well studied, but winter flocks are much larger than in the Marsh tit and have larger territories (Gaston **1973,** Glen and Perrins **1988).** One possibility is that the deciduous patches in the Bergslagen forests now are too small to contain this species. If so, a Long-tailed tit flock may subsist in one of the aggregated patches by utilizing part of a nearby patch as well. However, this hypothesis can not be tested without observations of individually ringed birds, or by radio-tracking. Moreover, Long-tailed tit flocks are made up of family groups and at least males tend to breed within the flock territory (Glen and Perrins 1988), which may indicate short dispersal.

In the Hazel grouse, juveniles settle into territories during their first summer and generally only disperse short distances (mean distance = **1.2** km; Swenson 1991c). Swenson (1991c) suggested that due to this, Hazel grouse should be susceptible to isolation. Birds then remain in these territories over winter and breed there. Thus, this species is ecologically similar to, for example the Nuthatch, and although there may have been some effect of patch size, the Hazel grouse was not affected by isolation. However, it is a much larger bird than the Nuthatch (300–400 g vs **20–22** g; J. Swenson pers.comm., Enoksson unpubl.) with larger territories. It may be that the larger bird uses the landscape in another way (cf. Angelstam and Mikusinski **1994).** Furthermore, although dependent on deciduous trees, Hazel grouse are less specialized than the Nuthatch and Marsh tit to ***mature*** deciduous forest. Further studies, using larger patches, are needed to evaluate the effect of habitat fragmentation in this landscape on Hazel grouse.

To conclude, the differences between the six species we studied, in response to isolation of deciduous patches within a coniferous forest, can probably be related to differences in dispersal pattern, social system outside the breeding season, territory size and degree of habitat specialization. However, further studies on the ecology of these species in this landscape are needed to fully untangle the causes behind the difference in response.

Birds and changing forest

For resident birds, the most serious effect of industrialized forestry is the severe reduction of the deciduous component in middle-aged and old taiga forest (Angelstam **1990, 1992,** Swenson and Angelstam **1993).** Older trees with trunks large enough to contain adequate nest holes are also an important factor of habitat quality for hole-nesting species, such as Nuthatch and *Parus* species. The insect fauna, which is an important part of the diet for many birds (Gaston **1973,** Perrins 1979), is richer in unmanaged forests and also in areas with a high abundance of deciduous trees (Ehnstrom and Waldén **1986).** Birds that require older deciduous forest have therefore declined (Aulén **1988,** Nilsson ***et al.*** **1992,** Berg ***et al.*** **1994)** and remain where forests have not been managed. About one third of the resident bird species are not present in the managed forests (i.e. most of the forest landscape) but are found only in small fragments where the natural succession pattern remains (Angelstam **1992).**

This impoverishment is most serious in older forest age classes. Today the average **80–100** year old patch only has 4% deciduous trees (Svensson **1980)** but in Bergslagen where forest management has a longer history, this proportion is 0.5% (Swenson and Angelstam **1993).** An important habitat is now the mixed deciduous/coniferous

forest that has developed on abandoned meadows and along forest-field margins during the last 40–50 years (Ihse **1993,** Ihse and Angelstam unpubl.). However, our study indicates that not only percent remaining deciduous forest is important, but also its distribution within the coniferous forest.

Conclusions

Mature deciduous trees are of great importance to many resident birds and so is the distribution of them. A highly fragmented landscape, with only small patches of deciduous forest separated by distances of some kilometers, negatively affects the distribution of resident bird species specializing on deciduous forest. Some species are affected to a greater extent than others. To maintain these species in our fauna it is essential to change present forestry methods so that the amount of deciduous forest increases and distances separating deciduous patches decreases.

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