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Effects of Forest Fragmentation on Reproductive Success of Birds in Boreal Forests

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ABSTRACT

The breeding success was studied experimentally using artificial bird nests. The pied flycatcher (*Ficedula hypoleuca* Pal.) was used as a study object when the effects of patch size, edges and vegetation characteristics on breeding success and distribution of individuals were examined. Only a minor influence of stand size and forest edge on nest predation was found. High edge-related nest predation existed only in the agricultural landscape where it was mainly caused by avian predators. In the forest landscape, nest predation concentrated to large stands as a function of an increased area of clear-cuts in the surrounding matrix. This was likely due to the penetration of rodent-eating mammalian predators to large stands to search alternative prey when vole populations crashed in the surrounding clear-cuts. The relationship between the nest predation rate and vegetation characteristics surroundings of a nest site was mainly associated with the visibility of nests. Sharp-designed man-made edges did not differ in nest predation risk from more feathered natural edges. At the macrohabitat level, pied flycatchers preferred large and medium-sized stands and avoided settling in small stands, which were mainly occupied by unpaired males. Males preferred edges of forest stands but avoided nest boxes situated right at the edge. The avoidance of small stands was possibly due to high costs of food search and the lower amount of food available in small stands. The costs of food search may also be essential when breeding in the extreme edge zone, since in these sites the suboptimal shape of the foraging area may increase the parents' flying distances in feeding the nestlings. At microhabitat level, adult pied flycatchers males inhabited territories with high numbers of deciduous trees while yearling males territories with high numbers of pines. The reproductive output was better in territories of adult males than in territories of yearling males. This age-related unequal distribution of males in relation to habitat quality was likely due to male-male contest over territories in which adult males dominate over yearlings forcing them to habitats of lower quality.

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List of original publications

This thesis is based on the following articles, which are refered to by their Roman numerals in the text:

I   Huhta, E. 1995: Effects of spatial scale and vegetation cover on predation of artificial ground nests. - Wildlife Biology 1: 73-80.

II   Huhta, E., Mappes, T. & Jokimäki, J. 1996: Predation of artificial ground nests in relation to forest fragmentation, agricultural land and habitat structure. - Ecography (in press).

III   Huhta, E., Jokimäki, J. & Helle, P.: Predation of artificial above ground nests - effects of edge structure, patch size and nest type. - Manuscript (submitted).

IV   Huhta, E., Jokimäki, J. & Rahko, P.: Despotic distribution of Pied Flycatcher (*Ficedula hypoleuca*) males in relation to habitat structure. - Manuscript (submitted).

V   Huhta, E., Jokimäki, J. & Rahko, P.: Edge effect on breeding success of the Pied Flycatcher (*Ficedula hypoleuca*) - an experiment. - Manuscript.

CONTENTS

1   INTRODUCTION

Habitats are naturally patchy. Habitat fragmentation in large scale occurs throughout disturbances mainly by fire and windfall (Pickett & White 1985). Forest fragmentation created by modern forestry and other human land use has strongly changed the structure of forests all over the world during past decades. This process has been particularly profound in tropical wet forests but also in temperate and boreal regions. Fragmentation of continuous, natural landscapes is one of the most important factors contributing to the loss of biological diversity (Wilcox & Murphy 1985). The loss of suitable habitat may decrease local populations to the size where stochastic events may cause the extinctions (Gilpin & Soule 1986). Therefore, it is not surprising why habitat fragmentation has become a key issue in conservation biology (Soule 1986).

Habitat fragmentation means a loss of original habitats, an increase of isolation and a decrease of the size of habitat patches. Fragmentation is injurious for the viability of species that favour interior areas of the forest, and for which the presence of edges is detrimental. On the other hand, the increased amount of edges may benefit species that favour edge habitats or that require more than one kind of habitat.

The ecological consequences of habitat fragmentation are diverse. It changes the structure and the quality of food resources (Helle & Muona 1985, Kremsater & Bunnell 1992). It changes the microclimate by altering temperature and moisture regimes (Matlack 1993, Young & Mitchell 1994). It changes availability of cover and structure of vegetation (Laurance 1991, Malcom 1994). Finally, it may affect the dispersal ability of animals and ecological interactions between species like the rate of nest parasitism, predation, competition, and contact with and exploitation by humans (Gates & Gysel 1978, Wilcove 1985, Andrén & Angelstam 1988, Johnson et al. 1992, Wauters et al. 1994). All these factors may affect considerably the persistence of populations, population trends of species, richness of the communities, and overall biological diversity of the ecosystem.

Landscape ecology is the study of the response of species or communities to patterns across more than one patch. Many of the basic tenets of landscape ecology originate from the theory of island biogeography

(MacArthur & Wilson 1967). However, aspects of the theory concerning real islands are not valid when studying the effects of terrestrial habitat fragmentation on species richness. Unlike real islands, habitat fragments are not surrounded by the sea or other hostile environment. Instead, fragments are in many cases open to influences from the surrounding habitat matrix and these effects may even be more important than processes occurring inside a fragment (Wiens et al. 1985). In addition, in island biogeography models, there is a mainland that is the source of colonists and immune to extinctions, and only populations on the surrounding islands show turnover.

Habitat fragmentation should be viewed as a complex process involving many components, including fragment size, habitat heterogeneity within fragments and surrounding matrix, and the edge effect (Wilcox & Murphy 1985, Andrén 1994). The size and amount of habitat patches in a landscape affect colonization, habitat use and persistence of individuals as well as the numbers of species occurring in the area. Individuals may use the habitat in a coarse-grained manner (Levins 1968) when their activity is concentrated on a single patch or each patch contains a local population. If individuals have large home ranges, they may use several patches inhabiting a landscape in a fine-grained manner (Levins 1968, Rolstad 1991). Also, individuals may be mainly restricted to one type of habitat being habitat specialists, for which the landscape structure is divided. Individuals may also use frequently many kinds of habitats being habitat generalists, for which the landscape structure is heterogeneously undivided (Addicott et al. 1987).

Reduction of forest stand size increases the amount of edge habitat between a forest and an open area. A generally accepted interpretation is that edges are characterized by high diversity and density of animals and plants (MacArthur & MacArthur 1961, Odum 1971). However, recent studies have shown that this is not always the case. Interactions between animals living in forest patches and surrounding matrix may sometimes cause effects that are not exclusively positive. Gates & Gysel (1978) demonstrated higher nest predation and interspecific nest parasitism risk among passerine birds breeding in edge habitats than in forest interior. The raised nest predation rate at an edge zone has also been reported in many studies with real and artificial nests (e.g. Chasko & Gates 1982, Andrén & Angelstam 1988, Kuitunen & Helle 1988, Møller 1989).

Forest fragmentation by forestry and the change in amounts of edge and interior habitats has been assumed to bring about considerable changes in forest bird communities throughout the world. This process has been assumed to be the major factor in the declining of some neotropical migrant birds in the eastern United States (Keast & Morton 1980, Wilcove 1985, Askins et al. 1990). Changes in forest bird communities have also been observed in northern Fennoscandia during the past decades. The density of many edge-preferring birds has increased and interior species declined (Järvinen & Väisänen 1979, Haila et al. 1980, Helle & Järvinen 1986).

I concentrate here to study the effects of forest fragmentation, in particularly forest patch size, the edge effect and vegetation structure on breeding success of forest birds. Reproductive success is the most important

factor affecting population trends of birds and it may vary depending on the quality of a habitat (Lack 1954, Møller 1991).

In this study artificial ground and above ground nests were used to assess experimentally nest predation risk of birds breeding in different kinds of fragmented landscapes and in stands of different size. A small passerine bird, the pied flycatcher (*Ficedula hypoleuca* Pal.) was used as a study object when studying the influences of a edge habitat, patch size and vegetation structure on breeding success and the distribution of individuals.

2 MATERIAL AND METHODS

2.1 Study areas

The studies presented in this thesis were executed around Meltaus Game Research Station in northern Finland (67°N, 25°E) and the study II partly around Konnevesi Research Station (62°N, 26°E) in central Finland. The northern study area is very sparsely populated. The landscape consists almost exclusively of forest stands of different sizes surrounded by open bogs and replanted clear-cuts of different successional stage. Scots pine (*Pinus sylvestris*) dominates with Norway spruce (*Picea abies*) and birch (*Betula spp.*) in the mixed forests.

In central Finland the landscape of the study area is divided into lakes, forest areas, agricultural land and small villages. There are also clear-cuts but not as large as in the northern study area. Norway spruce dominates coniferous forests intermixed with varying proportions of deciduous trees. Size of forest patch in both study areas varies from a couple of hectares to a few square kilometres.

2.2 The species

Potential nest predators in both study areas are red fox (*Vulpes vulpes*), pine marten (*Martes martes*), stoat (*Mustela erminea*), least weasel (*Mustela nivalis*) and red squirrel (*Sciurus vulgaris*). Badger (*Meles meles*) and raccoon dog (*Nyctereutes procyonoides*) are present only in the southern study area. Potential avian nest predator in both regions is raven (*Corvus corax*), in the northern area Siberian jay (*Perisoreus infaustus*) and in the southern area hooded crow (*Corvus corone cornix*), black-billed magpie (*Pica pica*) and European jay (*Garrulus glandarius*).

The pied flycatcher is a small (12-13 g) migratory passerine bird. It breeds in tree holes but it is also easily attracted to nest boxes. The territory of this

species is small containing only a nest hole and its immetiate surroundings. Males arrive to breeding areas at the beginning of May and immediately after that they occupy a nest hole and start to sing. Females arrive about a week later than males (Lundberg & Alatalo 1992). Flying insects are common food of the pied flycatchers but they also commonly forage in trees and on the ground. The most important food for adults and nestling are spiders, caterpillars and dipterans (Lundberg & Alatalo 1992).

2.3   General methods

2.3.1   Nest predation experiments (I, II, III)

Artificial bird nests were used in nest predation experiments. Nests situated on the ground contained two or more brown domestic hen's (*Gallus domesticus*) eggs. Nests above ground (open nests and nests in boxes) contained one domestic quail (*Coturnix coturnix*) egg.

The study areas were selected using aerial photographs (1:40 000) or, and topographic maps (1:20 000). Within study areas both large and small-sized forest stands were selected. Dummy nests were placed at edge areas and in interior parts of stands. Ground nests were placed usually under a small sapling or a brush that are typical nest sites for many ground breeding birds. Above ground nests were placed in small spruces or pines using a support made of wire. Nest boxes were situated in trees at the height of 1.5 m. Glovers and rubber boots were worn when placing nests to minimize human scent. Studies started at the beginning of June and nests were checked at daytime.

2.3.2   Landscape variables and habitat structure (I, II, III, IV)

Landscape variables used in all studies were stand size and the distance of a nest from the forest-open land edge. The percentage of farmlands around each nest site and the distance from the closest field were determined in the study II.

To assess vegetation heterogeneity, vegetation descriptions were made around each nest site except around nest boxes in the study III. Both structural and floristic variables of vegetation were measured. Structural variables recorded were mean height of trunks (m), timber volume (m^3/ha), the breast height diameter of trunks (cm), canopy cover (m^2/ha or %), structure of tree canopy, cover of shrubs (%), cover of open nests (%), and the visibility of open nests (m).
Floristic variables measured were the numbers of pine, spruce and birch and the numbers of junipers and coniferous, and deciduous shrubs. Percentage cover of brushwood and the area of barren ground were recorded in the study IV.

2.3.3 Invertebrate samples (IV, V)

To estimate the quality of an environment as a breeding habitat for pied flycatchers, invertebrate samples were taken using the sweep-net method. The samples were taken from the field layer, shrubs, saplings and lower branches of trees around each nest box. The samples were collected during the nestling period at the beginning of July. Abundance of invertebrates was estimated by means of the area sampled. Invertebrates were identified to the level of orders and classified into three size classes based on the body length (< 0.5, 0.5-1.0 and > 1.0 cm).

2.3.4 Biometry (IV, V)

All adult pied flycatchers were captured using traps inside the nest boxes. Birds were ringed, aged and weighed. Wing length (straightened chord), tail length and tarsus length were measured. Fledglings were weighed at the age of 13 d when they were leaving the nest. Fledgling mass has been used to determine the value of the offspring fitness in terms of their chances to survive to adulthood. The mean weight of fledglings was calculated on the per brood basis.

2.4 Spatial scale and nest predation (I)

In this study I examined how nest predation is related to spatial heterogeneity of the landscape by using two hierarchical levels of spatial scale landscape grain size and single stand size. First, landscape mosaics of fine, medium and coarse-grained were selected. Second, within each landscape type, small, medium and large-sized stands were selected. Artificial nests with four brown eggs were put in lines extending perpendicularly from forest road edges into the forest in each stand. Lines with a length of 100 m (containing 18 nests), 250 m (containing 36 nests) and 400 m (containing 54 nests) were put in stands of small, medium and large sized, respectively. Percentage cover of trees and height of dominant trees were assessed at the midpoint of each line.

2.5 Effect of surrounding matrix (II)

In this study we investigated the effect of the surrounding matrix of a forest patch on nest predation. We also studied the influence of vegetation structure on predation. The study was executed simultaneously in landscapes with large clear-cuts in Finnish Lapland and in landscapes with cultivated areas in central Finland. Dummy nests with two brown hen's eggs were placed at edges and interior areas of large and small-sized stands. Eggs were placed on a 0.4*0.4 m

board smeared with grease. In that way we were able to identify the predator types (avian or mammalian) robbed the nests. Vegetation descriptions were made around each nest. The visibility of nests for predators was also assessed.

2.6   Effects of edge structure and nest type (III)

The impact of man-made and natural edges on nest predation among passerine birds was studied. Because passerine birds have different kinds of nest types which may in turn affect the predation risk of a nest, four kinds of artificial nests were used. First, open nests made of moss without lining were used. Second, two kinds of open nests lined with domestic hen's white-brown feathers and reindeer's (*Rangifer t. tarandus*) hair were used. Third, nests in nest boxes without lining were used to assess predation risk of hole-nesting passerines. Nests were situated in two parallel lines at the interval of 50 m, one line along the edge zone and the other one in the forest interior about 100 m from the edge.

2.7   Habitat selection and breeding success in relation to habitat structure (IV, V)

The studies were carried out in summers 1992-1994. The study was carried out by erecting nest boxes at the edge and the interior area of forest stands of different size. We investigated what kinds of macro- and microhabitat pied flycatchers prefer as a breeding habitat and how breeding success is related to the structure of habitat. The macrohabitat represented forest stands varying in size and the edge-interior composition of stands. The microhabitat reflects vegetation structure surrounding each nest box within a stand.

Nest-boxes with similar size and quality were placed at different distances from forest edge to study how pied flycatchers choose their breeding territory in relation to the distance to forest edge. Further, experimental relocation of simultaneously paired pairs were performed to study the edge effect on breeding success. In this experiment initially pairs were let to occupy nest boxes situated at a distance of 50 m from the forest-open land edge. After that experimental nests were moved gradually during the nest building period towards the extreme edge area while control nests were moved towards the interior area of a stand. The moving was stopped when the experiment nests reached the edge (the distance of 0 m from edge) and the control nests the distance of 100 m from the edge.

3   RESULTS AND DISCUSSION

3.1   Spatial scale and nest predation (I)

Predation intensity in this study was extremely high; about 40 % of nests
(N=108) were robbed after the first two days and 95 % after seven days. At
landscape level, the total predation rate of nests was about equal between the
landscape types, although there was a trend that predation risk in stands
increased with increasing fragmentation (30.5 to 50.0 %). At stand size level,
predation was clearly higher in large stands (64.8 %) than in small ones. This
concentration also increased as a function of increased fragmentation of the
surrounding matrix since the highest depredation rate was detected in large
stands within the most fragmented landscape (94.4 %).

The unusually high nest predation pressure observed was probably
caused by the decline of vole populations during the preceding winter in the
study area. This decline can be well seen in the track densities of mammalian
predators derived from the wildlife triangle censuses executed in Finnish
Lapland (Helle et al. 1995).

The difference in the resource availability between forest stands and
the surrounding matrix may affect the habitat use of predators. Many rodent-
eating predators like foxes and small mustelids, may prefer to hunt in clear-
cuts during vole peak years, because the density of voles there is higher than in
closed forests (Hansson 1979, Lindström 1989).   However, when vole
populations crash in open areas, predators may penetrate to neighbouring
forest stands to hunt alternative preys (Angelstam et al. 1984). In this situation
a large forest patch could possible offer more food than a smaller one which
may explain predation pattern observed in this study. This assumption was
especially well supported by the observation that predation pressure was
highest in the large stands within the fine-grained landscapes where the
relative area of a open land was also highest.

3.2   Effect of the surrounding matrix (II)

In the forest-clear-cut dominated landscape the overall predation rate of artificial ground nests was not related to the distance from the forest-clear-cut edge or stand size. Instead, in the agricultural landscape nest predation was clearly increased in the edges in the proximity of fields. The edge nests situated very close to fields were preyed upon more often than the edge nests further away from fields. Among interior nests, such a relationship was not found. This effect was mainly brought about by avian predators (corvids) which preyed more edge nests near fields than mammalian predators. Furthermore, the proportion of nests robbed by avian predators was high in the agricultural landscape (76.0 %, N=25), whereas mammalians were the more important predator group in the forest landscape (61.8 %, N=55).

The areas intermixed with forest patches and farmlands are expected to be more productive containing more predators than forest dominated areas (Angelstam 1986, Andrén 1992). Moreover, the steepness in the productivity gradient between forest stands and surrounding open areas has been suggested to be the main factor causing elevated nest predation risk in forest edges. That is because many predators living in the surrounding matrix are expected to be capable to penetrate into forest stands or to use edges as travelling lanes (Andrén & Angelstam 1988). Many of these predators have been presumed to be avians, especially corvid species (Andrén et al. 1985, Andrén 1992).

The results of this study confirm two of these three hypotheses. The overall predation rate did not differ between the agricultural and the forest landscapes. We did not found any edge effect on nest predation in the forest landscape but it existed in the agricultural landscape. In the northern forests clear-cuts are quite unproductive habitats in most years maybe except in vole peak years when the densities of field voles can be very high (Hansson 1979). Thus, according to the productivity hypothesis, the edge effect may be absent in the forest landscape or exists only temporally in years when the density of voles is high in the surrounding clear-cut areas. Finally, as predicted, the proportional importance of avian predators was higher in the agricultural landscape than in the forest landscape.

3.3   Vegetation cover, nest type and visibility of nests (I, II, III)

A single branch placed above a dummy nest decreased robbing risk suggesting that nest site selection in relation to cover the habitat can provide is an important factor in nesting success of birds (study I).

In the study II predation risk was raised in nest sites with high number of pines and spruces. This effect may be related to the preference of predators over particular habitats. On the other hand, it might be also that open structure of the understory of pine forests in Lapland and spruce forests in central Finland may facilitate predators to find ground nests situated in such habitats easier.

In the study III, regardless of the edge type, significant differences in predation of nests in relation to the forest edge was not found, although the predation rate of nests were raised almost in every nest type groups. Furthermore, predation was not associated with the edge type. However, the improved visibility of nests in man-made edges due to more open vegetation structure, increased predation risk more in these habitats than in natural edges. This finding suggests that lack of vegetation cover might be an important factor exposing nests to predation. This effect, on the other hand, was not strong enough to produce differences in predation rates between the edge types. This suggests that high productivity of the later succession phase of edges may also increase predation risk possibly because predators are more attracted to such habitats.

Cover and high density of vegetation have been observed to decrease nest failures of birds because heterogeneous vegetation structure conceals nests efficiently (Bowmann & Harris 1980, Yahner & Wright 1985). Clear-cutting may affect vegetation structure of the remaining forest patches increasing the width of the edge habitat. The vegetation structure of the edge zone may thus be exposed to changing microclimatical conditions and any other disturbances coming from the neighbouring open areas (Matlack 1993, Malcom 1994). This may change the vegetation structure of remaining forest patches in a way which may affect the amount of vegetation cover for breeding birds.

Nest design and a nest site both affected predation risk. The nests in the boxes suffered from lower robbing risk than the open nests. Predation of lined and unlined open nests was quite equal. However, the nests lined with hair tended to be taken more often than the control nests without lining. Thus, it might that nest design may also affect to some extent robbing risk of bird nests since some building material may increase conspicuousness of the nests for predators (study III).

3.4   Breeding success in relation to habitat structure (IV)

At macrohabitat level, pied flycatchers preferred large and medium-sized stands and avoided very small stands. The nest boxes in the small stands were mainly occupied by unpaired males which also arrived later than other males. Reproductive success of breeding pairs was not affected by stand size.

At microhabitat level, old pied flycatcher males preferred nest boxes with high density of deciduous trees. On the contrary, yearling males occupied territories which had high numbers of pines. The territory quality was associated with the existence of these tree species since the deciduous tree dominated territories contained more invertebrate food than pine dominated ones. The reproductive output of old males was better than yearling males. This was presumably due to the high amount of good quality invertebrate food in their territory. This age-related unequal distribution of males was likely due to male-male contest over territories in which older males dominate over younger ones.

The results show that pied flycatchers try to maximise their fitness by selecting breeding habitats in which their reproductive output is highest. This choice operates in different spatial scales of habitat. The net benefit of reproduction seems to be higher in stands of large size and in areas with high number of deciduous trees than in very small stands and pine dominated habitats. Subordinate males were forced to breed in poor habitats. In these habitats the costs of reproduction presumably are higher than in good quality habitats. For example, although the overall density of invertebrates seemed to be constant across the range of stand size, the total amount of food is lower in very small stands. Thus, breeding in small forest patches may cause more costs due to increased food search distances or lower quality of food. The results are consistent with the predictions of the ideal-despotic model (Fretwell and Lucas 1970) which states that reproductive success of individuals is not equal along the quality gradient of habitats.

3.5   Edge effect and breeding success (V)

The nest boxes situated close to forest edge (50-100 m) were initially most preferred and birds avoided the nest boxes situated right at the edge (0 m). Although the overall reproductive success did not differ between the edge and interior groups, pairs at the extreme edge produced significantly lighter fledglings than pairs in the interior areas (edges 14.2 ±0.5 g (mean±SD), N=16 and interior 14.5±0.6 g, N=20, respectively). Moreover, females of edge pairs lost more of their body mass during the nestling period (edge females 1.9±0.8 g, N=16 and interior females 1.4±0.7 g, N=19, respectively).

The avoidance of nest sites near extreme edge area seems to be due to lower quality of these sites for breeding. Nest site choice was, however, not related to lower amount of food supply in the forest edge than in the interior area since the abundance and quality of food did not differ between the areas. Instead, it seems plausible that differences in parental care between the study groups may explain the results observed. However, because quality of parents was also controlled, it is probable that mass reduction of broods and females might be a result from environmental factors affecting the parental care.

According to the central place foraging theory (e.g. Andersson 1978), the optimal foraging area should be round. However, at the extreme edge the foraging area of pied flycatchers is a half circle in shape because they did not forage on open areas. Edge pairs are thus forced to increase the radius of their foraging area to obtain the same sized forested area as in the interior part of a stand which ,in turn, increases their travelling distances between foraging and nest sites. The increased travelling distance can be very costly for parents during nestling period when parents feed the nestling about every other minute (Lundberg & Alatalo 1992).

Thus, the direct fitness costs caused by breeding at the extreme edge would be an increased energy consumption and possibly increased predation risk as a result of longer flying distances. The indirect fitness costs would be

the lower quality of fledglings produced and possibly the lower survival rate and the lower reproductive value of parents in future.

4   CONCLUSIONS

The results of this thesis show that habitat quality is an important factor affecting reproductive success and fitness of birds. These environmental factors may also affect temporal variation in population densities, richness of the communities, and finally biological diversity of the ecosystem.

In most experiments presented in this study landscape variables such as patch size and edges had only a weak effect on -robbing risk of nests. Instead, structure of the surrounding matrix was more important affecting a predation rate. In the agricultural landscape nest predation seemed to be more edge-related than in the forest dominated landscape. In the forest landscape nest predation increased with increasing amount of clear-cuts in the surrounding matrix. At the same time also nest predation concentrated more to the large stands than to the small ones.

The predation rate by avian predators was higher in the agricultural landscape, while mammalian predators were more important in the forest landscape. Avian predators caused elevated predation risk at forest edges near fields. The assumption that total predation risk should be higher in agricultural landscapes because of higher productivity of that habitat than in forest dominated landscapes was not confirmed, since the total predation rate did not differ between the landscape types.

Clear-cutting of continuous forests has been assumed to increase total productivity of forest landscape which may, in turn, increase the numbers of predators in the area. Vole densities in peak years are high in clear-cuts and in these years mammalian predators may also favour these areas as hunting areas or living sites. However, the fluctuation of vole populations in northern Fennoscandia is considerable. This may also affect habitat use and diet of predators and it could be that in years with decreasing vole populations, predators may start to use more time in forest patches instead of clear-cutts to search alternative preys such as bird nests.

Thus, in the boreal ecosystem, temporal and spatial distribution of the main diet of predators in relation to given landscape mosaic must be taken into consideration in nest predation studies. According to the results of this study, I hypothesize that in vole peak years in coniferous forest habitat density of

predators and predation intensity would be higher in clear-cuts than in forest stands (Table 1). Furthermore, in these years edge- and stand size-related nest predation may exist to some extent. This might be due to generalist predators which prefer forest habitats but also use open areas searching for a prey. This pattern may also increase predation risk in edges of stands and in small forest patches surrounded by clear-cuts. On the contrary, in vole crash years predation pressure towards alternative preys should be high within forest stands. At that time only a weak edge dependence in nest predation could be expected since predators do not move across the edge area to an open habitat. Instead, stand size should be more essential since large stand could offer more alternative preys.

For birds like pied flycatchers, habitat structure affected habitat choice, breeding success and distribution of individuals. Habitat choice has often been studied on the basis of only one spatial scale like vegetation structure. However, the results of this study suggest that habitat choice of birds is affected by many levels of spatial scale and thus multiscale approach in habitat selection studies of animals may be more appropriate.

TABLE 1   Predicted predation pattern towards alternative prey items such as bird nests in fragmented boreal forests in relation to habitat structure and prevailing nourishment level (vole cycle).

Phase of vole cycle		Peak	Crash
Habitat component		**Predation risk**	
Matrix	forest	low	high
	open	high	low
Edge effect		exists	no
Stand size	large	low	high
	small	high	low

YHTEENVETO

Lintujen lisääntymismenestys suhteessa metsän pirstoutumiseen

Metsien käsittelyn aiheuttama metsien pirstoutuminen on maailman laajuinen ilmiö ihmiskunnan pyrkiessä lisääntyvässä määrin hyödyntämään maapallon resursseja. Metsien hakkaaminen aiheuttaa alkuperäisen metsähabitaatin vähenemistä, yhtenäisten metsäalueiden muuttumista saarekkeiseksi, jäljelle jäävien metsäsaarekkeiden eristymistä toisistaan sekä muutoksia saarekkeiden kasvillisuusrakenteessa. Metsäpinta-alan väheneminen aiheuttaa metsälajien häviämistä. Eliöstöä muuttaa myös ympäristörakenteen muuttuminen rikkonaisemmaksi, mikä puolestaan aiheuttaa lukuisia muutoksia eliöiden välisiin vuorovaikutussuhteisiin. Nämä ympäristötekijät vaikuttavat eliöpopulaatioiden säilymiseen, yhteisörakenteeseen, populaatiodynamiikkaan ja lopulta koko ekosysteemin monimuotoisuuteen.

Väitöskirjassani keskityn selvittämään, minkälaisia seurauksia metsien pirstoutuminen aiheuttaa metsälintujen lisääntymismenestykselle. Lisääntymismenestys on yksi kaikkein tärkeimmistä tekijöistä, jotka vaikuttavat eliöpopulaatioiden säilymiseen elinympäristössään. Oletan, että yksilöiden ja populaatioiden väliset erot lisääntymisessä muodostavat tärkeän tekijän, joka on metsäeliöyhteisöissä havaittujen yhteisö- ja lajistomuutosten takana. Käytin useimmissa tutkimuksissani kanan- ja viiriäisenmunilla varustettuja tekopesiä, joiden avulla tutkin petojen aiheuttamaa pesätuhoriskiä suhteessa metsäympäristön rakenteeseen. Lisäksi tutkin, miten metsän rakenne vaikuttaa kirjosiepon (*Ficedula hypoleuca* Pal.) pesimämenestykseen, ravinnon jakautumiseen ja yksilöiden sijoittumiseen pesimäalueelle.

Useissa lehtimetsä- ja maaseutualueilla tehdyissä tutkimuksissa metsän pirstoutumisen on havaittu lisäävän metsälintujen pesätuhoriskiä. Tämä johtuu metsäsaarekekoon pienenemisestä ja reunavaikutuksen lisääntymisestä, jolloin petojen on helpompi löytää pesät myös saarekkeen sisäosista sekä oppia käyttämään reunoja saalistusalueinaan. Tässä pohjoisella havumetsävyöhykkeellä tehdyssä tutkimuksessa metsäympäristön rakenteella oli suuri vaikutus pesätuhoihin. Pesätuhoriski kasvoi samalla kun avohakkuiden osuus maapinta-alasta metsäsaarekkeiden ympäristössä kasvoi. Lisäksi pesätuhot samalla keskittyivät suurempiin saarekkeisiin. Tämä johtui todennäköisesti myyriä pääasiallisena ravintokohteenaan käyttävien nisäkäspetojen keskittymisestä suuriin metsäsaarekkeisiin, kun myyräkannat avohakkuilla olivat romahtaneet. Maaseutuvaikutteisessa ympäristössä pesätuhot keskittyivät metsäsaarekkeiden reunoihin erityisesti jos saareke sijaitsi lähellä peltoa tai niittyä. Kokonaispesätuhoaste maaseutuympäristössä ei kuitenkaan eronnut

metsäisessä ympäristössä saadusta tuloksesta. Maaseutuympäristössä lisääntynyt pesätuhoriski metsänreunoissa johtui varislinnuista, sillä niiden osuus pesätuhoissa oli suurempi kuin metsäympäristössä.

Kasvillisuuden rakenteella pesän välittömässä ympäristössä oli myös vaikutusta pesän säilymiseen. Pesätuhoriskin suuruus oli useimmissa tapauksissa todennäköisesti sidoksissa pesän näkyvyyteen pedoille. Ihmissilmällä mitattu pesän näkyvyys ei kuitenkaan kovin hyvin selittänyt hävikkiä. On siis ilmeistä, että ihmisaistein tehdyllä mittauksella ei täysin voida arvioida petojen kykyä löytää pesää. Pesätuhoriski ei ollut suurempaa metsähakkuiden luomissa terävissä ja kasvistoltaan avoimemmissa reunoissa verrattuna rehevämpiin luonnonreunoihin. Pesän näkyvyys kuitenkin selitti parhaiten pesähävikkiä nimenomaan terävissä reunoissa.

Ensimmäisinä pesimäalueelle saapuneet kirjosieppokoiraat suosivat metsänreunoja pesäpaikkoinaan. Ne valtasivat useimmiten pöntön, joka oli sijoitettu noin 50-100 m päähän reunasta, mutta välttivät asettumista aivan metsänreunaan sijoitettuihin pönttöihin (0 m). Kokeellisessa työssä pystyin osoittamaan, että pesiminen äärireunassa aiheuttaa pareille enemmän kustannuksia kuin pesiminen sisempänä metsässä. Nämä kustannukset tulevat esiin poikueen ruokinta-aikana, jolloin emot joutuvat hyödyntämään muodoltaan epäedullista ruokailualuetta. Tämä lisää emojen lentomatkaa ravinnonkuljetuksessa pesälle, mistä seuraa suurempi ajankäyttö ja energian kulutus ravinnonhankinnassa. Seurauksena tästä oli naaraiden suurempi painon menetys ruokinta-aikana ja lähtöpoikasten huonompi kunto verrattuna metsän sisällä oleviin pareihin.

Kirjosiepot myöskin välttivät asettumista hyvin pieniin metsäsaarekkeisiin, vaikka hyvä pesäpönttö oli tarjolla. Nämä saarekkeet valtasivat pääasiassa viimeisinä saapuvat koirat, jotka hyvin usein jäivät parittomiksi. Pienten saarekkeiden välttäminen lienee myös yhteydessä tarjolla olevan ravinnon pienempään kokonaismäärään ja ruokailualueen koon ja muodon epäedullisuuteen. Vanhat kirjosieppokoiraat suosivat pönttöjä, joiden välittömässä ympäristössä kasvoi runsaasti lehtipuita. Nuoret koirat joutuivat tyytymään huonompilaatuisiin reviireihin, joilla kasvoi runsaasti mäntyä. Hyvillä lehtipuuvaltaisilla reviireillä parit tuottivat myös enemmän lentopoikasia. Tämä johtui todennäköisesti näiden reviirien tarjoamasta paremmasta ravinnosta, sillä erityisesti hämähäkkien ja kaksisiipisten hyönteisten määrien todettiin korreloivan positiivisesti lehtipuiden määrän kanssa.

Tämän tutkimuksen perusteella metsänhoidon kannalta monimuotoisen metsälinnuston säilymiselle olisi olennaista suurten avohakkuiden, suuren reunojen määrän ja liian pienen metsäsaarekekoon välttäminen. Metsämosaiikki, joka koostuu eri-ikäistä puustoa sisältävistä suurista ja keskisuurista metsäsaarekkeista sekä pienistä aukoista, täyttäisi parhaiten useimpien metsälintujen ympäristövaatimukset. On kuitenkin selvää, että yksityiskohtaisia tutkimuksia tarvitaan lisää erilaisten metsänkäsittelymenetelmien vaikutuksista eri eliölajien perusekologiaan.

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