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Effects of spatial scale and vegetation cover on predation of artificial ground nests

Esa Huhta

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Scale-dependent effects of landscape heterogeneity on predation of artificial ground nests were studied. Two spatial scales were selected: landscape grain size and single stand size. The landscape types did not differ from each other in their total predation intensity. Depredation was highest in larger stands in all the landscape types studied and the highest predation rate was detected in the largest stands within the most fragmented landscapes. This is possibly due to concentration of rodent-eating predators from surrounding open areas into large stands in the study year when their main prey, voles, crashed. In crash years, alternative predation on e.g. forest bird nests may play an important role for these predators. The influence of predators concentrating into forest stands is expected to be especially strong in landscapes of fine grain size because such a landscape contains relatively more open areas. The predation rate was independent of the distance of nests from the edges of forestry roads. Direct cover (a branch) placed above dummy nests improved the survival rate of these nests. However, tree canopy cover only had a slight effect on the predation rate. The lacking impact of canopy cover on nest predation may be due to the openness of the northern pine forests which makes it particularly easy for predators to discover dummy nests on the ground.

Key words: spatial scale, nest predation, vegetation

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Consequences of human disturbance on ecological processes at different landscape levels have been recently recognised as an important problem in ecology. Recent trends in landscape ecology have emphasised the need to take into consideration interactions between spatial patterns and ecological processes (Forman & Godron 1986, Krummel et al. 1987, Lavorel et al. 1993). Influence of the scale-dependence of landscape heterogeneity on ecological interactions has been little studied, despite the fact that many biological processes have been shown to be sensitive to scale (Kotliar & Wiens 1990, Rahel 1990, Johnson et al. 1992).

The fragmentation of continuous forests has been shown to increase nest predation of birds (Gates & Gysel 1978, Whitcomb et al. 1981, Ambuel & Temple 1983, Wilcove 1985). These results derive from studies executed in temperate forests and tropical wet forests, but especially in landscapes dominated by agricultural land

(Andrén & Angelstam 1988, Small & Hunter 1988, Møller 1988, 1991, Gibbs 1991). Reduction of habitat island size increases the length of edges. This has been shown to facilitate predators in finding bird nests in forest stands of small size because many small and medium-sized mammalian and avian predators use edge areas efficiently in their prey search (Angelstam 1986, Andrén 1992).

In a patchy environment, sites differ in their suitability to organisms. Birds prefer patches that provide plenty of food and/or cover for breeding sites. In such patches the density of breeding birds can be very high. The density of breeding birds depends on the resource availability in stands of different size. So nest predation intensity may also be affected by the density of breeding birds and patch size. The distribution and habitat selection of nest predators may thus vary depending on the spatial heterogeneity and productivity of landscapes. Larger patches are ex-

pected to offer more resources than smaller ones and to be more attractive living sites. The quality of a single patch may also be affected by the mosaic structure of the surrounding matrix, i.e. landscape grain size (Wiens 1976). Thus, ecological processes at a given scale may also be affected by events at other scales.

Because nest loss in birds can be very high (Lack 1968, Ricklefs 1969), nest site selection must play an important role in the reproductive success of birds. A common assumption is that birds should select nest sites that provide the best shelter against predators and thereby minimise the risk of reproductive failures (Martin 1988, Martin & Roper 1988). Structural heterogeneity and the density of vegetation have been shown to decrease nest failures considerably in studies with artificial nests (Bowman & Harris 1980, Yahner & Wright 1985). Spatial heterogeneity of overhead and lateral cover of a nest site may be important, especially in areas where the density of aerial nest robbers is high.

In this paper the first aim was to study scale-dependent effects of landscape heterogeneity on depredation of artificial nests in Finnish Lapland. Two hierarchical levels of scale were investigated: 1) grain size of landscape types, and 2) size of a single forest stand within different landscape types. I studied whether there are separate or simultaneous effects of stand size (small to large) and landscape type (coarse to fine grain) on the nest predation rate. Here the term grain size *sensu lato* is used to describe both landscape characteristics and movement patterns of organisms (Levins 1968, Wiens 1976). This is appropriate because the landscape types used are composed of smaller and larger patches in relation to the home range size of most potential nest predator species living in the area.

The second aim was to examine the importance of vegetation cover on predation rate. This was studied using branches as extra cover above dummy nests and making descriptions of habitat features in the vicinity of nests.

I used dummy nests following the method used in many other studies (e.g. Andrén & Angelstam 1988). Predation rates on artificial nests cannot be used in quantifying predation rates on real nests (Loiselle & Hoppes 1983, Storaas 1988). However, standardised sampling with dummy nests probably provides reasonable information on the potential risk of nest predation in different landscapes and habitat patches.

Study area

The study was carried out in 1988 and in 1991 around Meltaus Game Research Station in northern Finland (ca 67°N, 25°E). The study area consists mainly of forests and peat lands. Scots pine *Pinus sylvestris* dominates (68%) the mixed coniferous forests, where Norway

spruce *Picea abies* and birch *Betula* spp. make up 22% and 10%, respectively. A mosaic of forests, clear-cuts and open bogs create a patchy landscape. The size of forest patches in the area varies from a couple of hectares to a few square kilometres.

The potential mammalian nest predators occurring in the area are red fox *Vulpes vulpes*, pine marten *Martes martes*, stoat *Mustela erminea*, least weasel *Mustela nivalis* and red squirrel *Sciurus vulgaris*. Possible avian nest robbers are common raven *Corvus corax* and Siberian jay *Perisoreus infaustus*.

Methods

Study layout

When studying the effect of spatial scale on depredation of dummy nests in 1991, two hierarchical levels of scale were used. Firstly, the landscapes were divided into three types with respect to grain size (coarse [CGL], medium [MGL] and fine grain [FGL]) by the proportional existence of forest stands of different size (Fig. 1). The areas were selected so that they each contained at least 50% forest. The landscape types were determined from aerial photographs from 1985 (1:40,000) and topographic maps (1:20,000) using a frame scale of 3 × 3 km. Landscapes classified as coarse grain-type consisted mainly of large forest islands and had only a few open areas such as clear-cuttings and open bogs. In the other two landscape types forest stands were, on average, smaller and more isolated.

Secondly, the study areas were selected so that within each landscape type, both large, medium and small-sized stands were found (Fig. 1). The minimum sizes of the stands were ca 50 ha, 20 ha and 3 ha, respectively. Artificial nests with four brown domestic hen's *Gallus domesticus* eggs were placed along transect lines through each of these stands; in total 108 nests and 18 lines with six lines in each size category. The transect lines were drawn perpendicular to the forestry road's edge into the forest. These lines were 100 m long (containing 18 nests) in the small-sized stands, 250 m (36 nests) in the medium-sized stands and 400 m (54 nests) in the large-sized stands. The number of nests in each category is presented in Table 1.

The first nest of each line was placed at a distance of 10 m from the road edge. The distance between nests along each line was 50 m. Dummy nests were situated in places that are typical nest sites for capercaillie and other grouse species, e.g., under spruce saplings and junipers or at the base of tree trunks. Each nest was marked by a short red plastic ribbon tied around a branch or the tip of a stick placed about 10 m from the nest. The study was carried out during 3-13 June and the nests were checked

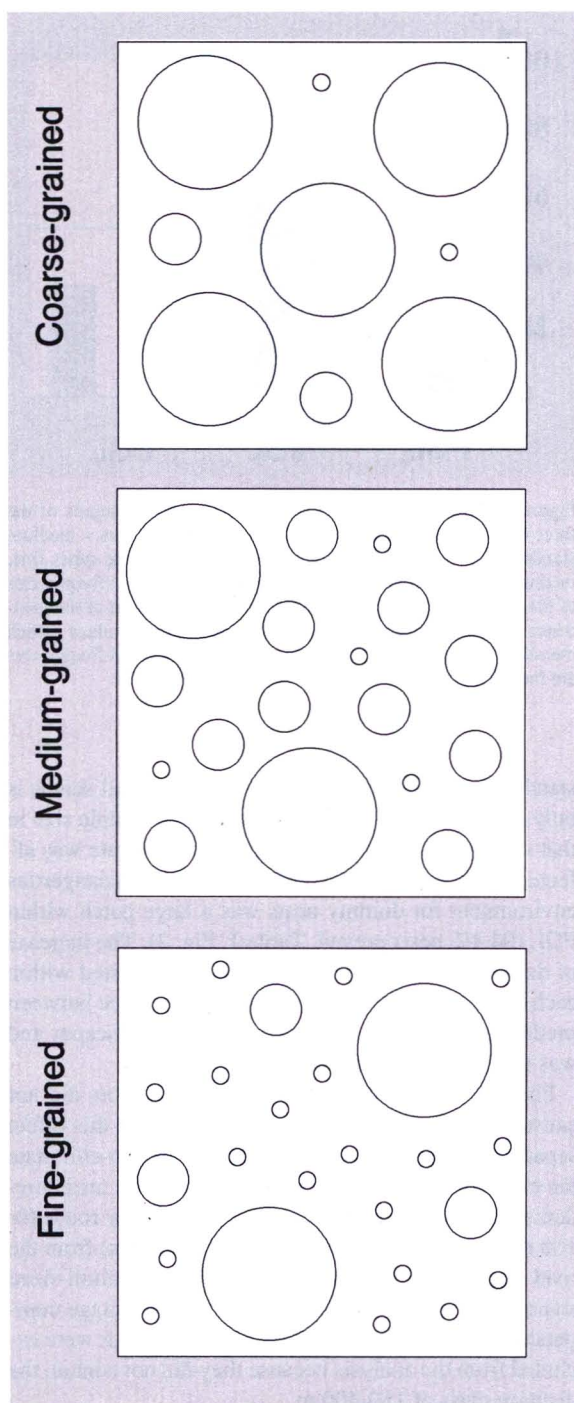


Figure 1. Schematic structure of the three landscape classification types used in the study.

three times during daytime within this period (on day 2, 7 and 10).

In the other experiment in 1988, 31 groups of artificial nests were placed at 200 m intervals along forestry road sides. Each group consisted of two nests each containing

Table 1. Proportions of dummy nests (%) preyed upon during two days, according to the landscape types (fine, medium and coarse grain) and stands (small, medium and large). Number of nests in parenthesis.

Grain type/ Stands	Landscape type			
	fine	medium	coarse	total
small	0 (6)	0 (6)	33.3 (6)	11.1 (18)
medium	8.3 (12)	58.3 (12)	0 (12)	22.2 (36)
large	94.4 (18)	50.0 (18)	50.0 (18)	64.8 (54)
Total	50.0 (36)	44.4 (36)	30.5 (36)	41.6 (108)

two brown domestic hen's eggs. The nests were placed separately on both sides of the road, at 5 and 25 m from the road bank. Of the 62 nests, 40 were placed in mixed spruce or pine-birch stands and 22 on open clear-cuts. Half of the nests were left uncovered, and half of them were covered by a 0.5 m long spruce branch. The branch obscured the view from directly above. Covered and uncovered nests were placed in random order along the road side. The study was conducted during 9-17 June and the nests were checked twice during this period.

Vegetation descriptions

In 1991, canopy cover structure of stands was assessed at the midpoint of each nest line by estimating selected variables within a circle with a 20 m radius. Along the longest lines (400 m) two measurement points were used. Recorded variables were the number and mean height of the dominant trees, proportion of canopy cover of each tree species, and percentage cover of the whole tree canopy. The boundary of the circle was marked in the field by putting sticks on the arc of the circle. The total number of trunks within this circle was counted. Canopy cover was assessed from five randomly selected points within each circle using a short pasteboard tube with a diameter of 4 cm, and a length of 10 cm. The height of the dominant trees was measured at these points using a hypsometer.

Statistical methods

The effects of the landscape type, stand size and vegetation structure on the depredation rate were analysed using log-linear, logit and logistic regression models (Hosmer & Lemeshow 1989). In the logit-analyses the predation rate (PR, preyed/unpreyed) can be explained with categorical or continuous variables. The model best fitting the data receives the highest P-value. Contingency tables and χ^2 -test were used with Yate's continuity correction in assessing the impact of cover and nest site on depredation. All analyses were performed using the SYSTAT statistical program package (Wilkinson 1990).

Results

Effect of scale

In 1991, all nests were preyed upon during a period of 10 days. About 40% of the nests were robbed after the first two days and 95% after seven days. Because the predation intensity was very high only the data available after the first nest check (two days) were used in the analysis.

In the analysis I used hierarchical logit-models where the predation rate (PR, the response variable) was explained by the landscape type (LT) and stand size (SS). I used a backward selection method in which I started the analyses from the fully saturated model. The saturated model ($PR = LT + SS + LT \times SS$) included all the interactions between variables and the model fits the data completely ($P = 1.0$). Because none of the logit-models with less interactions, e.g. models $PR = LT + SS$ or $PR = LT$ and $PR = SS$, fitted the data set ($P = 0.0$ in each case), I chose the saturated model to describe the data. The interpretation of the logit-model is that the variates LT and SS jointly affected the response PR.

I fitted several log-linear models of independence to the data to examine the relationships between variables in more detail (Table 2). The table shows that the predation rate was independent only of the main effect of the landscape type. Predation was thus more dependent on stand size than on landscape type. However, the log-linear model describing the independence of all three variables ($PR + LT + SS$) did not fit the data, indicating a strong interaction between these variables ($P < 0.001$, Table 2). This means that stand size alone did not have an independent effect on predation because the predation rate in stands of different size was also strongly dependent on the landscape type in which the stand was situated (Fig. 2).

The adjusted residuals of this latter model are presented in Fig. 2. Residuals measure the deviation between observed and expected frequencies of the model. In FGL the predation rate was higher in large stands and lower in small and medium-sized stands than predicted by the model. In MGL the predation rate was lowest in small stands, while in CGL it was lowest in medium-sized

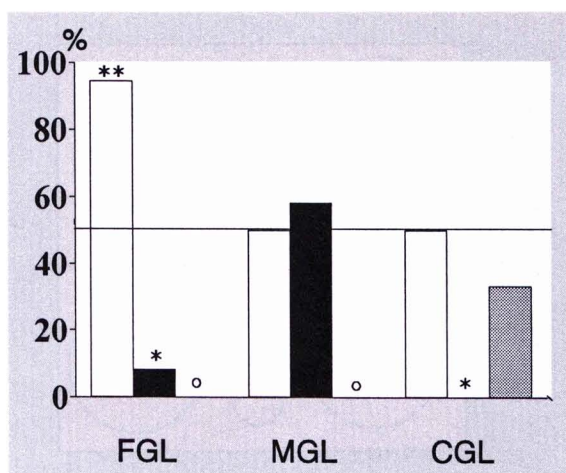


Figure 2. Relative predation rate observed in forest stands of the three different sizes (open bars = large stands, dark bars = medium stands, light bars = small stands) within the landscape types fine, medium and coarse grained. The line depicts expected frequencies of the log-linear model fitted and indicates the contrast of independence. Significant deviations of adjusted residual values which measure the deviation between observed and expected frequencies are indicated, 0 = $P < 0.10$, * = $P < 0.05$, ** = $P < 0.01$.

stands. The reason why the difference in small stands is only near significant ($P < 0.10$) is that the sample size in that case is too small. In FGL the predation rate was affected most strongly by stand size. The most dangerous environment for dummy nests was a large patch within FGL (94.4% nests preyed, Table 1, Fig. 2). The increase of depredation with increasing stand size existed within each landscape type. However, the dependence between predation and stand size varied between landscapes and was thus affected by the landscape type, too.

Forestry roads with narrow treeless corridors did not cause any edge effect in this study. I studied this effect separately between stands of different size to eliminate the effect of stand size from the analyses. The mean predation rate was no higher on nests placed near roads (0-100 m) than on those further away (150-400 m) from the road edge (in large stands 50%, and in medium-sized stands 22%, respectively; the basis for percentage computation was 18 nests in each case). Small stands were excluded from the analysis because they did not contain the distance class of 150-400 m.

Table 2. Results of the log-linear models (1-4) used to test the independence of the variables, predability rate, stand size and landscape size. Only model 2 fits the data, thus indicating that the predation rate is independent only of the main effect of the landscape type.

Variable	G	df	P
1) Predation rate + stand size + landscape type	58.3	12	0.0
2) Predation rate + landscape type	3.0	2	0.2
3) Predation rate + stand size	26.0	2	0.0
4) Constant	45.0	4	0.0

Effect of cover

Nests covered by branches suffered significantly lower predation than open uncovered nests (covered nests: 32.3% preyed, uncovered nests: 83.9% preyed; $\chi^2 = 14.9$, $P < 0.001$, Table 3). However, predation intensity did not differ significantly between nests placed in forests and

Table 3. The effect of extra cover (covered nests) on predation of dummy nests in open (clear-cuts) and forested habitats (see the text for details). The number of nests is given in parenthesis.

	Preyed	Unpreyed
Uncovered nests	83.9 (26)	16.1 (5)
Covered nests	32.3 (10)	67.7 (21)
Clear-cuts	54.5 (12)	45.5 (10)
Forests	60.0 (24)	40.0 (16)

open clear-cuts (60.0% and 54.5% preyed in forests and in clear-cuts, respectively; $\chi^2 = 0.02$, $P > 0.10$, Table 3). Even when examining the nest site effect among uncovered nests only, the nest position (forest or clear-cut) did not affect the robbing rate ($\chi^2 = 0.0$, $df = 2$, $P = 0.95$). Thus, canopy cover of trees did not provide any significant shelter against nest robbers in this experiment.

The cover structure of stands did not differ between habitat islands of different size. However, larger stands seemed to have more pine and less spruce than smaller stands (mean percentage cover of pines in small stands: $38.8 \pm 33.2\%$ S.D. and in large stands: $75.8 \pm 35.6\%$ S.D., $t = 1.9$, $df = 8$, $P = 0.07$; spruce in small stands: $50.0 \pm 38.9\%$ S.D. and in large stands: $15.0 \pm 25.1\%$ S.D., $t = 1.9$, $df = 8$, $P = 0.06$). The test was made using arcsin-transformed values.

A linear logistic regression model was constructed to examine the influence of the vegetation cover characteristics on the predation rate (Table 4). A stepwise backward procedure was used in which the likelihood ratio

Table 4. Logistic regressions between cover variables and depredation of nests. All parameters are tested using a stepwise backwards procedure. The likelihood ratio chi-square test, based on the difference in deviance (G) between two models, is used to assess the effect of each cover variable on the predation rate. Only birch cover affected the predation rate. The relationship between the continuous independent variable and the logit is quadratic.

	G	df	P
Full model	5.1	5	>0.10
Cover variables:			
Number of trunks	0.0	1	NS
Canopy cover	0.3	1	NS
Height of trunks	0.5	1	NS
Spruce cover	1.1	1	NS
Birch cover	3.3	1	NS
Birch cover + (Birch cover) ²	4.0	1	<0.05

Selected model: $G(\chi^2) = 0.08 (\pm 0.8) + 0.47(\pm 0.39)$ birch cover - $0.03(\pm 0.02)$ birch cover²

chi-square test, based on the difference in deviance between two models, is used to assess the effect of each variable excluded from the model. The cover of pines was too heavily correlated with other variables and was excluded from the model. Only birch cover had a significant negative effect on the predation rate.

Discussion

To understand ecological interactions, we must know how these relationships are influenced by the spatial configuration of the entire mosaic of habitat patches. A hierarchically structured landscape may interact with ecological processes in many ways. The grain size and the mosaic structure of forest landscapes affect ecological patterns, because stands of different sizes differ in their suitability and resource levels for organisms. Fragmentation decreases the size of forest islands and increases the amount of edges. Reduction of the forest island size has been shown to increase the predation rate in many studies with both real and artificial bird nests (Andrén et al. 1985, Wilcove 1985, Small & Hunter 1988, Møller 1991). In other studies the results have been reversed (Langen et al. 1991), or there has been no relationship at all (Storch 1991).

In this study, nest predation was affected by two levels of scale. Between the landscape types there was no difference in the total predation rate although there was an indication that the predation risk would be highest in FGL (50.0%, Table 1). This was because nest predation in FGL concentrated more on large-sized forest stands than in MGL and CGL. In MGL nests were lost in medium and large-sized stands whereas in CGL nests were lost in large and small stands only. The smallest stands suffered predation only within CGL. Correspondingly, when examining effects of small scale (stand size) the predation rate was clearly concentrated on larger stands in every landscape type. Furthermore, the predation rate was highest in the largest patches in almost every case except in MGL (Table 1, Fig. 2).

In this study, predation intensity was much higher than that found in southern Fennoscandia (Andrén et al. 1985, Angelstam 1986). The very high predation rate of artificial nests (40% robbed after 2 days) observed in this study may be a result of the shift of rodent-eating predators to alternative prey such as the eggs and nestlings of forest birds when their main prey declines in number (Angelstam et al. 1984).

Northern Fennoscandian vole populations fluctuate cyclically. During the study period in the summer of 1991, the vole populations declined in southern and central Finnish Lapland (A. Kaikusalo unpubl.). This was reflected in the relative densities of mammalian predators, too (Table 5).

Table 5. Track densities given as numbers of tracks/10 km/24 hours for the most commonly occurring mammalian predator species based on results obtained during the wildlife triangle censuses executed in the Finnish Lapland during the winter 1990-1992. (Helle et al. 1995).

	1990	1991	1992
Red fox	6.4	3.5	3.8
Pine marten	1.2	0.7	0.6
Stoat	6.4	2.0	2.7
Least weasel	0.6	0.5	0.2

To explain the high predation rate in large forest patches several elements must be taken into account. The difference in resource availability between forest islands and the surrounding matrix may affect habitat use by predators. For predators, like the pine marten, inhabiting mature forests, clear-cuttings and open bogs are less preferable habitats (Pulliainen 1983, Snyder & Bissonette 1987, Lindström 1989). However, many rodent-eating predators (e.g. red fox and the small mustelids) may prefer to hunt in clear-cuttings because the density of voles is higher there than in closed forest patches (Hansson 1978, Henttonen 1987, Lindström 1989). The high predation rate in large stands could be due to a concentration of small and medium-sized predators into those stands when the vole populations have crashed in surrounding open land-areas. This pattern can be observed in every landscape type but is not so clear in CGL where predation was observed in the largest and smallest stands only. The lack of depredation in medium-sized stands in CGL may be incidental.

I have no data on predator densities or the habitat use of predators in different kinds of landscapes. The total predation rate was similar between the three landscape types although it was highest in FGL (Table 1). It seems plausible that the higher predation pressure in larger stands is mainly due to foraging by predators concentrating into larger stands in poor nourishment years. It is likely that a large forest patch with a high resource level (food) would be a more preferable habitat for most predators than smaller patches. Small stands might be inhabited only by subordinate individuals, forced to live or forage in small suboptimal patches. The amount of non-forested areas and the number of small stands are highest in FGL. In such an environment the concentration effect of predators or their hunting into larger stands may be greater than in a more forested landscape as found in this study. Thus, the habitat utilisation of many small and medium-sized predators in northern coniferous forests can be considered to be coarse-grained (Wiens 1976) which means that predators use only a certain habitat type at any one time. In good vole years clear-cuttings and bogs are the

most preferred habitats whereas in poor nourishment years large forest patches offer alternative prey items.

In agricultural landscapes in southern Fennoscandia, predation was primarily due to corvid species deriving from farmlands and meadows surrounding forest patches (Andrén 1992). In this study, I did not identify predator species. Thus the proportion of nests preyed upon by mammalian and avian predators is unknown. However, data are available from an experiment with dummy nests performed in the same area in 1992 (Huhta et al. unpubl.), which show that mammalian predators constitute the most important group of nest predators (86% of nest loss).

It is possible that the relative importance of mammalian and avian predators varies between years. However, the wildlife triangle censuses show that densities of the most common mammalian predators in the area are high, especially in good nourishment years. Thus, it is a fair assumption that mammalian predators played an important role in the loss of dummy nests in the area. Scents that may have been left by the investigator may also mean that mammalian predators find nests more easily than avian predators. This problem is, however, largely avoided in this study because only the results after the first nest-check are taken into account.

Nest density affects predation rate if predators perform an area-restricted search after having found a nest as suggested by Tinbergen et al. (1967). Conflicting results have been reported from studies concerning density-dependence of nest predation. A trend towards higher predation risk has been verified at higher nest density (Reitsma 1992), whereas others have found no density-dependence (O'Reilly & Hannon 1989). Differences in the predator communities present in different studies may explain the opposing results. In this study, the likelihood of predators encountering a nest line have been kept constant by putting more nests into larger stands. Therefore, the density of nests per unit area is similar in every stand despite different stand sizes.

I could not determine any edge effect of nest predation in this study. This is possibly due to the structure of my edges which were not edges in the true sense, as between forests and open lands, instead the open areas were relatively narrow corridors along forestry roads. It seems that forest predators do not use forestry road sides in the same way as they do when they are hunting edges between open and forested areas (Gates & Gysel 1978, Wilcove et al. 1986, Andrén & Angelstam 1988, Gibbs 1991).

Spatial heterogeneity of vegetation and cover of nests are important in reducing nest predation (Bowman & Harris 1980, Yahner & Wright 1985, Angelstam 1986, Yahner & Cypher 1987). In this study, only the cover of deciduous trees had a slight negative effect on nest loss. The nest robbing rate did not differ; not even between the nests placed in open clear-cuts and those placed in forests. On

the contrary, the survival rate of nests was improved by direct cover (a branch). A shrub layer mainly provides foliage cover directly for ground nests, and may play a more important role than the canopy cover of trees. The northern boreal forests are rather open and consist mainly of Scots pine with a poorly developed and sparse shrub layer. Stands such as these are relatively thin and the visibility of objects for predators is thus better. In addition, the domination of pine in larger stands in the area, may lead to increased nest losses.

The efficiency of searching tactics of different predators may be affected by vegetation structure. While avian predators rely mostly on visibility, mammals may also use scent. How effective each searching tactic is in different kinds of environments has not been studied here. In northern Fennoscandia, Scots pine dominates forests, whereas thick spruce forests are common in the southern region. Thus, openness of forest habitats may facilitate especially avian predators in finding nests.

In conclusion, the predation intensity of dummy nests may be affected by the functional response of predators towards alternative prey items when their main prey is declining. In this study the highest predation rate was observed in the largest stands in the most fragmented landscapes. Thus the structure of the landscape may strengthen this process. However, the data in this study originate from a rather atypical year when the population of voles crashed. Further studies would reveal whether the patterns observed here would be the same under different nourishment conditions.

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