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Predation on artificial ground nests in relation to forest fragmentation, agricultural land and habitat structure

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The impacts of forest fragmentation agricultural land and habitat structure on depredation of artificial ground nests were studied in the cultivated area in central Finland and in the forest dominated area in Finnish Lapland The overall predation rate did not differ between the regions The overall predation rate was also independent of landscape characteristics forest patch size and the distance to patch edge However, nest predation was clearly affected by the agricultural land since the robbing rate in forest edges was higher near farmlands than further away This effect was caused by avian predators which proportional importance in predation was higher in the agricultural landscape than in the forest landscape In both regions, depredation correlated positively with high numbers of pine and spruce This can be mainly explained by the preference of predators over coniferous forest habitat as a living or hunting area

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Forest fragmentation created by forest management and other land use has been shown to affect community structure and population dynamics of birds and mammals (e g Whitcomb et al 1981, Ambuel and Temple 1983, Hunter 1990, Saunders et al 1991) Consequences are mainly due to increased loss of forest area and isolation of remaining forest islands Among birds, this process has contributed to negative outcomes both for interior and edge-breeders and possibly even excluded some forest species from heavily fragmented areas (Helle and Jarvinen 1986, Martin 1988, Askins et al 1990) Edge breeders have suffered from reduction of forest patch size although this process increases the amount of an edge habitat This is because many nest predators are also able to use edges as hunting areas or transitory zones which in turn increases risk of nest damages (Gates and Gysel 1978, Wilcove 1985, Small and Hunter 1988, Møller 1989)

In agricultural landscapes intermixed with farmlands and small forest patches, the effects of fragmentation would be especially harmful because the density of predators and predator pressure towards bird nests would be higher than in forest dominated areas (Angelstam 1986, Andrén 1992) In cultivated areas predation pressure is mainly due to abundant corvids living in fields and meadows at the surroundings of forest stands These open-land predators are also able to access small forest fragments or use agriculture-forest edges efficiently in their prey search (Andrén and Angelstam 1988) Thus, stronger edge and patch size related nest predation would be expected in agricultural landscapes than in forest landscapes

In the boreal forests the surrounding matrix of forest patches consists mainly of bogs and clear-cuts Furthermore, large forest patches are also frequent In these landscapes the predator faunas and predation patterns

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may be different since the structure of the environment is not so fine-grained and habitat types differ from that of agricultural landscapes

Nest predation may also be affected by habitat features that are described at smaller spatial scales High cover and structural heterogeneity of vegetation have been found to prevent nest failures in many studies with dummy nests (Yahner and Wright 1985, Niederleitner 1987) Forest fragmentation affects vegetation since the structure of vegetation may vary in relation to woodlot size and to the distance from forest edge (Laurance 1991, Malcom 1994) The densities of small bushes and trees of different age are often higher near forest edges than in interior parts of forest stands This increases the amount of cover and spatial heterogeneity of vegetation which may in turn affect predators' habitat use or ability to locate bird nests (Bowmann and Harris 1980)

In this paper the following hypotheses derived from previous studies of fragmentation and nest predation were tested 1) nest predation rate is higher in small forest fragments and in edge areas than in large patches and in interior areas, 2) the predation rate was affected by surrounding matrix of forest patches, predation should be higher and nests preyed mainly by avian predators in agricultural-forest mixed areas than in forest dominated areas, 3) risk of nests to be preyed upon is related to cover and vegetation structure in the vicinity of a nest site

Study areas

The study was executed in two areas in the agricultural-forest mixed landscape in Konnevesi, central Finland (62°N, 26°E) and in a forest dominated landscape without agricultural land in Meltaus Finnish Lapland (67°N, 25°E) The northern study area is very sparsely populated The landscape consists almost exclusively of different sized forest stands surrounded by open bogs and clear-cuts In central Finland the landscape is fragmented by agricultural lands, lakes and small villages There are also clear-cuts, but not so large as in Lapland The vegetation structure of forests differs strongly between the regions In Lapland the forest is dominated by Scots pine *Pinus sylvestris*, whereas Norway spruce *Picea abies* dominates in central Finland The density of shrubs and tree canopy cover were also higher in central Finland The main differences in vegetation characteristics between the study areas are presented in Table 1

Predator faunas

Potential mammalian nest predators in both regions 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 procynoides* are present in the south only Among avian predators, common raven *Corvus corax* occurs in both regions Siberian jay *Perisoreus infaustus* occurs only in the northern area In central Finland there are hooded crow *Corvus corone cornix*, black-billed magpie *Pica pica* and European jay *Garrulus glandarius* which are strongly associated with farmland-forest landscapes

Methods

Study layout

Use of artificial nests in nest predation studies has been criticised because the predation intensity on dummy nests and the type of predators may differ from those of real nests (Storaas 1988, Willebrand and Marcstrom 1988) However, because many bird nests are hard to find, artificial nests are the easy way to experimental work on nest predation In addition, female birds try to select nest sites which optimise their reproductive success, thus dummy nests are also the only way to control the variety of natural nest sites

Within both study areas large and small forest stands were selected using aerial photographs (1 40000) The actual size of the large fragments was at least 50 ha and the small ones 7–10 ha Two artificial nests with two brown domestic hen's eggs were placed into each stand on a 0 4 × 0 4 m board The board was smeared with a layer of grease on which predators left foot-prints (Angelstam 1986) Tracks were identified as left by mammalian or avian predators only because in many cases the tracks were so fuzzy that we were not able to identify species Gloves and rubber boots were worn when placing and checking nests to minimise human scent

Most nest predation studies with artificial nest suggest that the "edge effect" usually occurs within 50 m of

Table 1 Means and standard deviations (±) of habitat variables in agricultural landscape (south) and in forest dominated landscape (north) Statistical test Mann-Whitney U-test

	South (N = 40)	North (N = 40)	p
Cover variables			
Cover of a nest (%)	53 9 (30 1)	47 6 (30 6)	NS
Shrub cover (%)	6 9 (9 3)	3 1 (3 8)	0 001
Tree canopy cover (%)	54 3 (16 2)	31 6 (20 0)	<0 001
Horizontal visibility (m)	10 1 (3 9)	11 4 (4 8)	NS
Vegetation variables			
Pines total (%)	5 1 (8 9)	40 3 (30 1)	<0 001
Spruces total (%)	59 6 (17 9)	30 0 (21 2)	<0 001
Deciduous trees total (%)	35 2 (17 8)	29 7 (21 4)	NS
Number of shrubs	15 0 (12 0)	6 3 (6 8)	<0 001
Tree density	35 9 (14 8)	35 9 (16 1)	NS

an edge (Paton 1994) Within each stand we used one nest in the edge area (0–5 m) and one in the interior part of a stand (150–200 m from an edge) Older edges, as those maintained by agriculture, usually have a better developed understory than younger edges such as those created by the forestry (Hunter 1990, Angelstam 1992) In Lapland most of our edges used were clear-cut/forest edges and only in some cases the edge type was more natural (open bog/forest) In central Finland both forest-clear-cut, and forest-agriculture edges were used Furthermore, we included in the study only open areas which were at least 100 m in width Thus, the quality of openings used fulfilled the requirements proposed by Paton (1994)

Forty nests were placed in both study areas Nests were put under a small sapling, which is a typical nest site for ground breeding grouse species In that way we could standardise the quality of a nest site, which may also affect the encounter rate of nests by predators Every nest was marked in the field using a short red plastic ribbon tied around the tip of the stick placed about 10 m from the nest The study was executed simultaneously in both study areas and it lasted until June which is the breeding time of grouse species Nests were checked after 7, 14, 21 and 30 days of exposure at daytime Eggs that disappeared (in every case both were taken) were interpreted as depredated

The percentage proportion of fields was estimated within a circle radius of 1 km around each nest site (N = 40) using topographic maps (1 20000) The proportion of farmland around nest sites was 0% in Lapland and ranged between 0 and 32% in central Finland The distance from each nest site to the closest field was also measured

Vegetation descriptions

The vegetation descriptions were made using two nest centred circles with a radius of 5 and 10 m The smaller circle was used when measuring the features of the shrub-layer (height of <2 m) The shrub-layer variables measured were the number of junipers, coniferous and deciduous shrubs, the total number of shrubs and shrub cover The stand variables and canopy cover were assessed within the large circle The stand variables recorded were numbers of pines, spruces and deciduous trees Canopy cover of trees (%) was based on five selected point-sightings The assessment was made through a short pasteboard tube, diameter of 4 cm and length of 10 cm One of the measure points was placed directly above the nest to assess the upper sided canopy cover of the nest The other four points were placed on the arc formed by the large circle in rectangular directions from the nest

The horizontal visibility of a nest was estimated walking along transects extending outward from the nest in the four cardinal directions At each transect the distance (m) from the nest to the point where the nest was just passed out of sight was recorded The mean of these four distances was used as a visibility value for each nest in the analyses

Statistical analyses

Each nest was considered as an independent observation Several multiple logistic-regression models were constructed in the data analysis The logistic regression converts binary data into probability values by fitting logistic curve through the available points The parameters of the logistic model were estimated by maximum likelihood The impact of each landscape and habitat variable on nest predation was studied using the forward stepwise procedure Dependence between variables was also analysed using two dimensional contingency tables with G tests All statistical analyses were performed with the SYSTAT (Wilkinson 1990) and SPSS (SPSS 1992) statistical program packages

Results

Effects of landscape and habitat variables

We retained in the multiple logistic regression model all landscape and habitat variables and all two-factor interaction terms between the region and the variables This was made because the features of forest vegetation differ considerably between the study areas, and therefore it should be possible that the environmental factors may have different kind of impact on predation within the regions (Table 1) Number of pines and spruces was the most important environmental factors affecting nest predation and they explained together 48% (pseudo R^2) of the variation in the model selected (Table 2) The predation risk of nests was high in sites with high number of these tree species The two-factor interaction terms region × pine and region × spruce were not significant indicating that the relationship between tree variables and the predation rate was parallel between the regions

No significant improvement of the explanatory ability was found by adding the landscape variables i e stand size or distance to the edge in the model (Table 2) Overall, the predation rate of nests was rather equal in stands of different size and in relation to edge (in small and large stands 55% and 45% preyed, N = 40, respectively, at edge and in interior areas 50% and 50%, preyed, N = 40, respectively, Fig 1a, b, Table 3) Also, the predation rate in relation to edge was similar within stands of different size (in large stands 47% and 53% preyed at edges and interior areas, N = 17, respectively, in small stands 50% and 50% preyed, N = 21, respectively)

Table 2 The multiple logistic regression model of the relationship of landscape and habitat variables to predation All variables were tested with a stepwise forward procedure The likelihood ratio test was used to assess the effect of each variable (G) The logistic model selected is $g(x_i) = -2\ 1\ (\pm 0\ 65) + 0\ 2\ (\pm 0\ 05) \times$ pines $+ 0\ 07\ (\pm 0\ 03) \times$ spruces

Variable	G	df	p	pseudo R^2
Distance from an edge	0 5	1	0 819	0 0
Stand size	1 3	1	0 251	0 0
Region	1 9	1	0 168	0 0
Canopy cover	0 0	1	0 957	0 0
Cover of shrubs	0 1	1	0 814	0 0
Cover of a nest	0 4	1	0 536	0 0
Visibility of a nest	1 4	1	0 245	0 0
Number of shrubs	0 3	1	0 571	0 0
Number of deciduous trees	0 4	1	0 521	0 0
Number of spruces	1 0	1	0 318	0 0
Number of pines	9 5	1	<0 01	26 7
Interactions				
Region × Distance	0 7	1	0 387	0 0
Region × Stand size	3 5	1	0 060	12 1
Region × Canopy cover	0 7	1	0 418	0 0
Region × Cover of shrubs	0 2	1	0 682	0 0
Region × Cover of a nest	0 0	1	0 934	0 0
Region × Visibility	2 7	1	0 100	8 2
Region × Shrubs	0 1	1	0 743	0 0
Region × Deciduous trees	0 1	1	0 778	0 0
Region × Spruces	3 8	1	0 051	13 1
Region × Pines	9 3	1	<0 01	26 3

Variable	G	df	p	pseudo R^2
Selected model	18 7	2	<0 001	
Number of pines	18 4	1	<0 001	27 3
Number of spruces	7 4	1	<0 01	20 9

The multiple logistic regression was used again to analyse whether the predation type (avian or mammalian) was affected by the landscape and the habitat variables Using forward stepwise analysis we found that only the region had a significant effect on predator types In the agricultural landscape the proportional importance of avian predators was clearly higher than in the forest dominated landscape in Lapland (Table 3)

Effect of the agricultural land

The percentage proportion of farmlands close to nest stands had no effect on the predation rate Instead, among edge nests the predation rate was elevated in stands situated very close to fields than in stands further away ($G = 7\ 5$, $df = 1$, $p < 0\ 01$, Fig 2) Among interior nests such a relationship was not found ($G = 0\ 7$, $df = 1$, $p > 0\ 5$, Fig 2) This effect was caused by avian predators (corvids) which preyed upon significantly more edge nests near agricultural land than mammalian predators (logistic regression avian predators $\beta = -0\ 004$, $\pm 0\ 003$, $G = 3\ 8$, $df = 1$, $p = 0\ 05$, mammalian predators $\beta = -0\ 001$, $\pm 0\ 002$, $G = 0\ 9$, $df = 1$, $p > 0\ 10$)

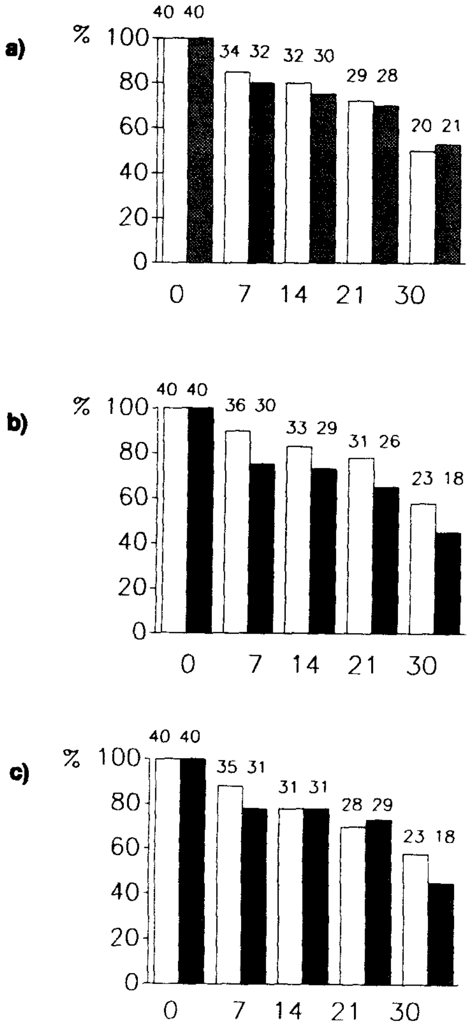

Fig 1 Remaining ground nests (%) after 0, 7, 14, 21 and 30 d of exposure a) in relation to the distance to forest/open land edges (interior hatched), b) to the size of forest patches (small hatched) and c) to the latitude (north hatched) Numbers above columns indicate numbers of nests

Table 3 Proportion of dummy nests robbed by avian and mammalian predators in relation to forest stand size, nests' distance from an edge and to the region Only the regio had the significant effect on nest predation ($G = 4\ 6$, $df = 1$, $p < 0\ 05$) The sample size (N) indicates total number of nests robbed in each category

N	Stand size		Position		Region	
	large	small	edge	interior	south	north
	17	21	19	19	17	21
Avian	23 5	33 3	26 3	34 6	47 1	14 3
Mammalian	76 5	66 7	73 7	68 4	52 9	85 7
Total rate	44 7	55 3	50 0	50 0	44 7	55 3

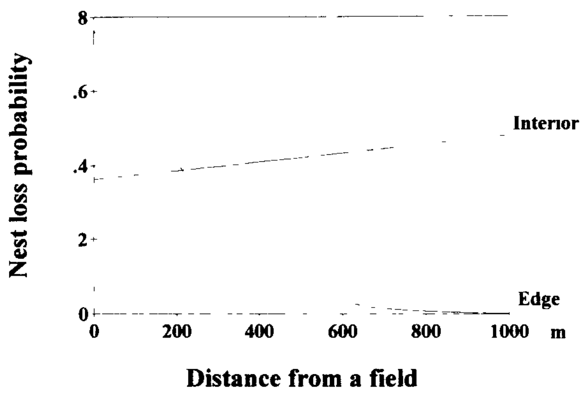

Fig 2 Logistic curves representing the probability of nests to be preyed upon at edges and in interior areas in forest stands as a function of the distance from farmlands Logistic models for edge nests $g(x_i) = 1\ 7\ (\pm 0\ 76) - 0\ 0076\ (\pm 0\ 004) \times$ (distance from fields) and for interior nests $g(x_i) = -0\ 5\ (\pm 0\ 8) + 0\ 0005\ (\pm 0\ 002) \times$ (distance from fields)

Discussion

Effects of fragmentation and agricultural land

The results of this study strongly suggest that the quality of matrix is an important factor influencing nest predation of ground breeding birds The "edge effect" in nest predation was found in agricultural-forest mixed landscapes where the matrix consists mainly of fields but not in forest-clear-cut dominated landscapes The predation rate was independent of the amount of agricultural land surroundings of nest stands but instead, the closeness of a field area increased clearly the robbing rate of the nests situated in edges This confirms the previous assumption that some predators living in field areas are also able to use edges in their prey search

Angelstam (1986) and Andrén (1992) concluded that the steepness in the productivity gradient between forest stands and surrounding open matrix is the main cause increasing predation pressure at the edge zone of forest stands In the agricultural areas non-forested matrix is rather productive habitats as compared to clear-cuts and bogs in forest landscapes This is due to supplemental food resources provided by human in matrix areas of agricultural landscapes Thus, field areas intermixed with forest patches may also include high numbers of predators which in turn may induce high predation risk towards bird nests in agricultural landscape as compared to landscapes surrounded by degraded habitat (Andrén et al 1985) However, we were not able to confirm this later assumption since the total predation rate did not differ between the study areas

Our results agreed with those of Andrén et al (1985) that high nest loss in agricultural areas is mainly due to high density of corvid species Especially the role of hooded crows, jays and magpies in nest predation increases when the landscape becomes more agricultural dominated (Andrén 1992) In this study, high nest predation risk near farmland areas was namely caused by avian predators presumably corvid species The proportional importance of avian predators was also higher in central Finland than in Lapland supporting the results of the previous studies

Bird predators like corvids are visual searchers whereas mammalian predators may also use scent Since we used grease covered boards as nest sites to identify predator types, it may have facilitated some predators to locate nests easier However, this effect of the experimental procedure is equivalent since we used the same method in both regions, and therefore it should not affect predation rates differentially

In Lapland composition of the landscape is the matrix of forest patches surrounded by clear-cuts and open bogs with variety of size This habitat might, on average, be more unproductive than field-forest ecosystem Low prey densities in surrounding open areas of forest fragments may also explain the lack of edge dependence in nest predation in Lapland It might be that in forest-clear-cut dominated landscapes predators may not use habitats on both sides of the edge which may in turn decrease vulnerability of edge nests to predation

On the other hand Hansson (1979) has stated that the overall carrying capacity of forests fragmented by clear-cuts is higher than that of continuous forests because in vole peak years the densities of voles can be very high in clear-cuts In these years, clear-cuts could also be the favoured habitats by many rodent-eating predators (Lindstrom 1989) This situation could, however, exist only seasonally because in northern Fennoscandian populations of microtine rodents fluctuate cyclically Correspondingly, during a shortage of main preys predators may spend more time in forest stands than in surrounding open matrix to search alternative prey items like bird nests (Angelstam et al 1984, Huhta 1995) Thus, predation intensity of bird nests within forest stands may also vary seasonally depending on nourishment level of surrounding matrix

We could not find any evidence that predation pressure would be affected by forest patch size in either of the study areas In Lapland the nests situated in small stands became robbed more than the nests situated in large stands but the difference was rather slight Andrén and Angelstam (1988) suggested that a high perimeter-area ratio and small size of forest stand are the most important factors increasing predation risk in forest fragments The actual size of stands used in this study varied from over 50 ha to 7–10 ha The stands were thus clearly larger than stands used in the studies in the temperate forest area It could be that the variation of stand size in the present study was too narrow to cause any size dependent influence on the depredation rate Andrén (1994) concluded that a significant area dependent effects on population dynamics and thus ecological interactions may not occur until the proportion of original habitat of landscape has declined to as low as less than 10–30% of the total area of landscape If this expectation is valid, fragmentation in our study areas may be too coarse-grained to cause any negative ecological interactions such as elevated nest predation in forest patches

Effects of vegetation structure

Nest vulnerability to predation may be increased if a nest site is visible to predators Factors affecting visibility of nests like spatial heterogeneity of vegetation, foliage and ground cover have been shown to affect the survival rate of artificial nests in many studies (Bowman and Harris 1980, Angelstam 1986, Leimgruber et al 1994) These factors are also important in depredation of natural nests and in nest site selection of birds (Brittas and Willebrand 1991, Storch 1991, O'Schieck and Hannon 1993) The fact that we failed to found a direct correlation between visibility of nests and predation may be simply due to difficulties to assess real visibility of nests to predators Our method was maybe not fully appropriate when assessing conspicuousness of nests to different predator groups because mammalian and avian predators may have different kinds of visual field They may also possess different kinds of prey search tactics, for example, avian predators may locate nests while scanning from perches along habitats

Vegetation features associated positively with predation were numbers of pine and spruce This correlation may be partly caused by good visibility of nests in pine and spruce dominated forests The vegetation in understory of old conifer forests in both study areas is sparse Pine dominated heaths are rather barren habitats without thick shrub-layer and dense ground vegetation which decreases the amount of vegetation cover Also, old spruce forests (especially in the southern study area) are characterised by closed canopies which overshadow efficiently the ground surface preventing the growth of the thick shrub-layer Thus, in these habitats lack of the shrub-layer and the scarcity of field layer may facilitate predators in finding nests situated on the ground easier

The distribution of life requisites for predators may be affected by forest patch size, structure of surrounding matrix and habitat structure within the patch In fragmented landscapes, predators may use as living or hunting areas certain habitat patches with high resource availability Spruce dominated forest patches are common in agricultural areas and they are favoured habitats for many avian and mammalian predators like jays and red squirrels (Andren 1992, Andren and Delin 1994) These species are also potential nest predators and this may increase the robbing risk of dummy nests in spruce dominated stands especially in central Finland

Predators may concentrate their activity in areas according to productivity of a habitat or they may "spillover" from neighbouring productive habitats to barren ones Oksanen et al (1992) or use some habitat as transitory areas only According to Oksanen et al (1992), in the years with good nourishment level such as vole peak years in our study areas, barren habitats as pine forests would be occupied by many subordinate predators like small mustelids In these years small and middle sized predators might be more concentrated in pine heaths, and thus the higher chance to encounter bird nests could also be expected by, e g small mustelids in their search for voles Correspondingly, during vole crash years predators may spend more time to search alternative prey items especially in large forest stands which are, in general, pine dominated heaths in our study areas

In sum, a less studied problem is how ecological processes are related to different scale levels in a hierarchically structured landscape Here we demonstrated that both the macrostructure (fragment size, edges, surrounding matrix) and the microstructure (vegetation) of landscapes had an effect on nest predation pattern Predation of dummy nests was also strongly affected by the local predator community existing in the area Because of that, it is justifiable to conclude that it is not relevant to apply the earlier results of nest predation studies executed in temperate forest areas to the boreal forest ecosystem

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