

Vertebrate distributions relative to clear-cut edges in a boreal forest landscape

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Keywords: mammals, birds, boreal forest, clearcut, edge, distribution

Abstract

Clearcutting is the main method of harvesting boreal forests, to some extent mimicking natural disturbances by fire and wind-felling. Effects of clearcutting on vertebrate fauna in managed forests was examined by small mammal trapping in spring and autumn, winter censuses of mammal snow tracks and censuses of birds in spring and summer in one central and one edge (125 m) section of large clearcuts and mature forests, respectively. There was a separate clearcut fauna, at least on large clearcuts, that was well distinguished from the forest fauna. There was not any physiognomic ecotone but the forest fauna showed a marked edge effect with larger numbers of many species in the peripheral parts of the forest. In the forests examined, with a Western European bird fauna, there were no typical interior forest species, in contrast to northern taiga forests. The present forest species easily changed distributions seasonally and according to variations in snow conditions and food abundance. Such generalist species in the boreal forest will therefore vary considerably in local density according to landscape composition but will also show large-scale persistence. They may have been selected for as a result of man's restructuring of temperate and boreal landscapes, *e.g.* by forest management. Edge effects seem to arise for several reasons but will probably only apply to generalist species.

1. Introduction

Boreal forest landscapes have always been structured by disturbances. Pristine forests were governed by fire dynamics, and to some extent by storm-felling, (van Wagner 1987; Hytteborn *et al.* 1991; Hansson 1992). Managed forests have a counterpart in clearfelling and reforestation. However, the two types of disturbances usually differ, at least in the early phase, by smaller amounts of remaining woody vegetation in clearcuts as well as nutrient relationships and plant species composition (*e.g.* Niemi and Probst 1990).

In both situations some species move out from the forest into the disturbed open areas to exploit resources and possibly secondarily to colonize these

disturbed habitats. Due to the long history of large-scale disturbances in boreal forests, certain species may have developed adaptations for primary use of such disturbance patches. Other species may occupy similar early succession habitats elsewhere. However, boreal forests, as we now know them, have only existed for about 10,000 years and specialization or speciation may not account for present species associations entirely. Thus, animals utilizing disturbance patches or clearcuts should also occupy older forests and exploit their resources, to some extent. This means that disturbances or clearcutting may cause edge effects in parts of old or economically mature forests that border clearcuts. Similarly, parts of disturbance areas or clearcuts that are closest to forests may be

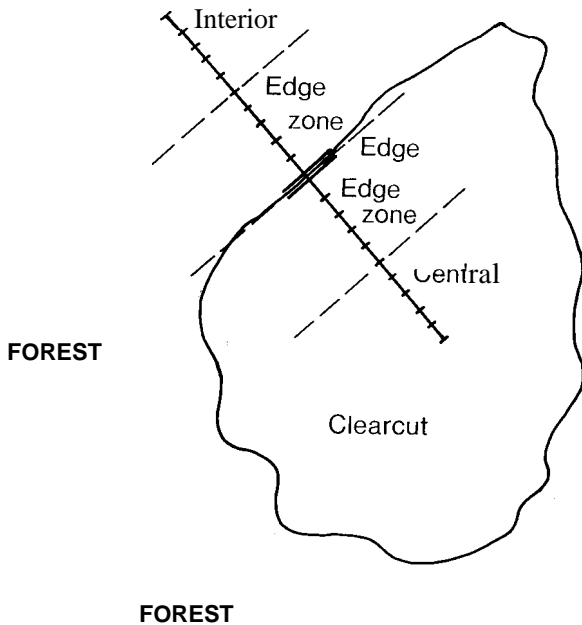


Fig. 1. General picture of the forest landscape examined. Clearcuts were at least 500 m in diameter. Census lines extended 250 m inside forest and out on clearcuts and were marked every 25 m. The lines were divided into four sections (each 125 m), with central and peripheral clearcut areas and peripheral and interior forest areas. The peripheral areas were considered as edge zones in the analyses. The very edge (the edge line \pm 2.5 m) did not demonstrate any clearly deviating numbers of mammals or birds.

used more by forest animals. Forest edges bordering clearcuts are usually abrupt but may show especially high productivity due to increased insolation and reduced competition. Clearcut edges close to forests may similarly have a contrasting vegetation due to shade and snow accumulation. Depending on clearcut sizes and distributions, neighbouring forest parts may develop locally specific faunas that affect the species composition in entire landscapes (Bendell 1974; Angelstam 1992).

This study is intended to illuminate edge effects on mammals and birds in a typical managed boreal forest landscape with large clearcuts in central Sweden. First I examine which species show differences in numbers between clearcuts and forests. Secondly, I ask if central and edge parts of clearcuts and forests deviate in number or distribution within the same species. The edge line was especially examined for density differences. I try to explain such

differences by the degree of specialization or use of special resources by the various species. I also examine if deviating distributions in specific habitat segments can be explained by interspecific interactions.

2. Methods

2.1. General design

Six large clearcuts, at least 500 m apart, were selected for study in a large forest area about 30 km west of Uppsala in south-central Sweden. The ground consists of fairly poor till and supports pine (*Pinus sylvestris*) – spruce (*Picea abies*) forests that are economically mature for felling in many parts. The clearcuts examined had been harvested in 1978 or 1979 and were regenerated with pine. The shortest axes of these clearcuts were at least 500 m. Lines extending from 250 m out on the clearcuts to 250 m inside the surrounding mature forest were demarcated at every 25 m (Fig. 1). The vegetation was carefully examined in September 1982 and September 1990 in a 100 m² square around each of these 25 m points on four lines used for small mammal trapping.

2.2. Small mammal trapping

Small mammals were trapped in late April and late September from September 1981 to April 1992 (11 years). Two snap traps were placed at every 25 m point for 14 days and inspected daily for three days and at three-day intervals for the remaining period. An extended trapping period was applied as the field vole (*Microtus agrestis*), common on clearcuts, usually has a lower trappability than other small mammals (Hansson 1975).

2.3. Snow tracking

Mammal trails in the snow were counted in December-March every morning after a snow-fall during the preceding day. These censuses were per-

Table 1. Distribution of various vegetation types on central (C) and edge (E) halves of census lines in forest and clearcut in September 1982 and 1990.

	1982				1990			
	Forest		Clearcut		Forest		Clearcut	
	C	E	C	E	C	E	C	E
Blueberry-moss	13	11	9	11	13	11	1	2
Bogs, boulders	7	9	8	6	7	9	7	7
Grassland	0	0	3	3	0	0	12	11

formed on all six sampling areas from 1981 onwards but had to be discontinued in the winter of 1987–88 (totally 7 years of census) as there was too little snow during all the following winters to permit any reliable tracking.

I recorded all trails crossing my straight ski tracks, which ran parallel and close to the marked lines. The same track was not skied on consecutive days as certain animals preferred to follow the old ski track for a while. Snow tunnels dug up to the snow surface by small mammals were counted within a 2.5 m distance from the ski track. Each track-crossing and snow tunnel between the 25 m marks was taken as one unit.

2.4. Bird censuses

Bird censuses were performed along the 500 m lines in principle according to the line transect methodology by Jarvinen and Vaisanen (1977), *i.e.* on a 25 m wide main belt to either side of the line and survey belts extending further out in the same habitat. The studies were performed every spring from 1980 to 1992 (13 years). Summer (July–August) censuses based on total observations rather than on singing birds only, were made in 1980–81 and 1988–89 (4 years). Data from the first year, including censuses also at other seasons, were presented by Hansson (1983). However, here I only compare total observations, summed across years, from both belts within 125 m intervals of the lines (*cf.* Fig. 1).

2.5. General analyses

I first compare total numbers observed on four line segments consisting of five 25 m intervals, *viz.* a central and a peripheral clearcut area and an interior and a peripheral forest area (Fig. 1) with X^2 statistics. In cases of significant differences, clearcut and forest parts were first contrasted and later on also central and edge parts of the forest and clearcut habitats, respectively. Observations at the very edge (± 2.5 m), including small mammal trap catches, were also examined for relative abundance. Detailed statistics are not reported when total numbers observed are provided in tables.

The distributions of observations were also compared between the first five years versus the remaining study period for small mammals and birds as the clearcut changed from a more or less tree-less open area to a forest regeneration and early sapling stands.

3. Results

3.1. Habitat distributions

The mature forest trees did not change noticeably in height while young pines on clearcuts grew to c. 2 m in height in 1992. The forest floor was mainly covered with a blueberry-moss carpet, with occasional small bogs and boulder fields. The blueberry-moss cover changed gradually on the clearcuts into dense grasslands, dominated by *Deschampsia flexuosa* and *D. caespitosa*. Thus there was more grassland on the clearcuts in 1990 than in 1982 (Table 1). Still, the habitat composition did not differ in any obvious way between central and edge parts of either forest or clearcuts.

3.2. Small mammal catches

The distribution of small mammal catches between the various forest and clearcut sections did not differ between the first and second five-year period. However, more *M. agrestis* and *Sorex araneus* were caught during the first period and more *Clethrion-*

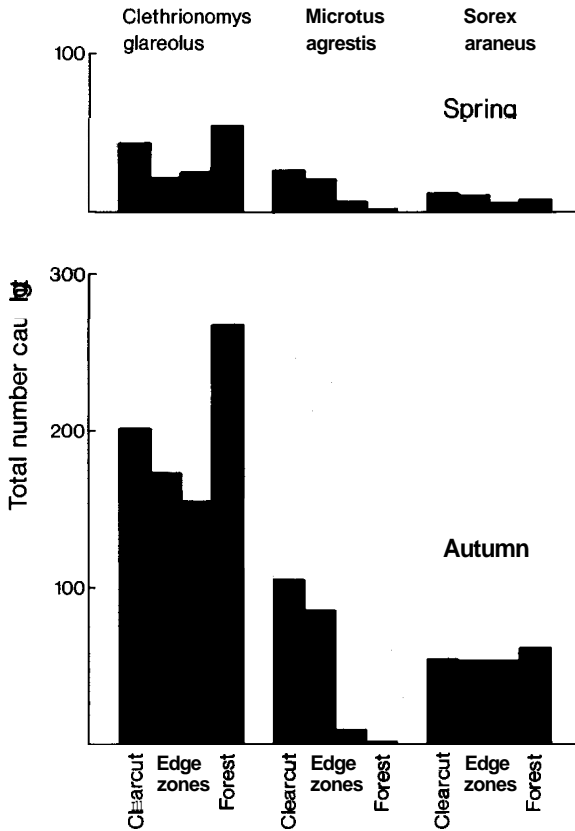


Fig. 2. Total catches of the three main small mammal species, separated into spring (above) and autumn catches (below). Clearcut and forest sections denoted according to Fig. 1.

nomys glareolus during the second one.

Capture distributions were compared separately for spring and autumn samples as few but mature animals were caught in spring and many but mainly immature animals in autumn. There was no significant deviation in numbers in either season at the very edge between forest and clearcut. During all seasons and years only a few specimens were caught of *Apodemus flavicollis* (totally 8), *Myopus schisticolor* (3) and *Neomysfodiens* (1).

Both bank voles *C. glareolus* and field voles *M. agrestis* demonstrated pronounced habitat differences in the spring captures (Fig. 2). *C. glareolus* ($X^2 = 21.03, p < 0.001$) had peak occurrences in the central parts of the clearcuts and in the interior parts of the forest (both different at $p < 0.001$), while *M. agrestis* ($X^2 = 33.60, p < 0.001$) was mainly caught on the clearcut and in similar pro-

Table 2A. Total distribution of snow tracks from winter censuses in 1981–87. Edge parts of clearcuts extended 125 m outward from the forest border and edge parts of forests extended 125 m inward from the forest border.

Species or type	Clearcuts		Forest	
	Central	Edge	Edge	Interior
<i>Alces alces</i>	121	85	56	70
<i>Capreolus capreolus</i>	235	280	524	345
<i>Vulpes vulpes</i>	48	56	57	58
<i>Martes martes</i>	13	12	31	31
<i>Mustela erminea</i>	32	26	7	6
<i>Mustela nivalis</i>	52	36	0	4
<i>Lepus timidus</i>	248	271	394	388
<i>Sciurus vulgaris</i>	0	0	58	67
<i>Apodemus</i> tracks	15	12	7	2
<i>Sorex</i> tracks	2	2	12	10
Vole tracks	143	128	142	148
Small mammal snow tunnels	32	36	2	4

portions on inner and outer sections. *C. glareolus* tended, thus, to avoid a wide area around the forest edge while few *M. agrestis* penetrated the forest. The common shrew *S. araneus* individuals did not show any significant deviations in their distributions. Seven *S. minutus* were caught in spring and all inside the forest.

C. glareolus showed a similar deviating distribution in autumn ($X^2 = 43.34, p < 0.001$) as in spring, but was comparatively more common deep inside the forest in autumn ($X^2 = 29.73, p < 0.001$). The clearcut differences were not fully significant in autumn. *M. agrestis* demonstrated also in autumn a preponderance on clearcuts and only few animals inside the forest ($X^2 = 166.64, p < 0.001$). *S. araneus* was at least as evenly distributed in autumn as in spring. *Apodemus sylvaticus*, which was almost only caught in autumn, showed significantly lower numbers in interior forest areas (6%) than in all other segments ($n = 52, X^2 = 10.84, p < 0.05$). It is obviously a clearcut species that penetrates only outer parts of forests. Only 14 *S. minutus* were caught but they were more common in forests than on clearcuts ($X^2 = 4.57, p < 0.05$). The small sample did not permit any analysis of distribution within habitats.

Table 2B. Significant deviations from random distributions of mammal tracks in the gradient Central clearcut – Interior forest. The name of the species or group is located in the section with the significantly highest abundance and the significance level at the final significant division (see text for explanation) is denoted. The species are ranked from Central clearcut section to Interior forest section and from highest to lowest significance level.

Differences between habitats	Species	Differences within habitats	Species
Clearcut	<i>Mustela nivalis</i>	Central clearcut	<i>Alces alces</i>
	< 0.001		< 0.05
	Snow tunnels		
	< 0.001		
Forest	<i>Mustela erminea</i>	Forest edge	<i>Capreolus capreolus</i>
	< 0.001		< 0.001
	Mouse trails		
	< 0.001		
	<i>Sciurus vulgaris</i>		
	< 0.001		
	<i>Lepus timidus</i>		
	< 0.001		
<i>Martes martes</i>			
< 0.01			
Shrew trails			
< 0.01			

3.3. Snow tracking

The study sites could be tracked for 8–12 days per year on new snow. About 4,500 signs were recorded altogether in 1981–1987 (Table 2). Trails of mink (*Mustela vison*) and badger (*Meles meles*) are not considered in the following analyses as the mink trails were strongly connected to a small stream and badgers were only observed in March when they had just left hibernation sites. No species or track type showed any concentration to the very edge.

Moose (*Alces alces*) showed a significant difference between the four habitat compartments. There were more moose tracks on clearcuts than in forest and more moose tracks in central than in edge parts of the clearcuts (Table 2B). Roe deer (*Capreolus capreolus*) also showed significant differences in track numbers between sections, and the edge sections of the forest had a much higher number of trails than the interior forest. Roe deer also moved more within forest than on clearcuts during winter.

The red fox (*Vulpes vulpes*) showed, totally, a very even distribution of trails. Martens (*Martes martes*) were mainly observed within forests without any differentiation between edge and interior.

In contrast, ermines (*Mustela erminea*) and least weasels (*M. nivalis*) were almost completely restricted to clearcuts.

The mountain hare (*Lepus timidus*) was totally most common in forest, without any evidence of substructuring within the two habitats. The squirrel (*Sciurus vulgaris*) was completely restricted to forest and it appeared equally common in interior and edge forest parts.

The combined vole (*C. glareolus* and *M. agrestis*) trails occurred in similar numbers in the four compartments. Tracks of wood mice (*Apodemus* spp.) and shrews (*Sorex* spp.) showed no substructuring within habitats, but were more common in clearcuts and forests, respectively. Snow tunnels made by small mammals (probably mainly by *M. agrestis*, Hansson 1986) were most common on clearcuts, but did not differ in numbers between outer and inner parts of the clearcuts.

The fox almost disappeared from the study area during 1984–1986 due to an outbreak of sarcoptic mange disease (Lindstrom and Morner 1985; Lindstrom 1991). Particularly many fox trails were observed in 1982, probably as a result of heavy mange infection, that appears to make the foxes especially

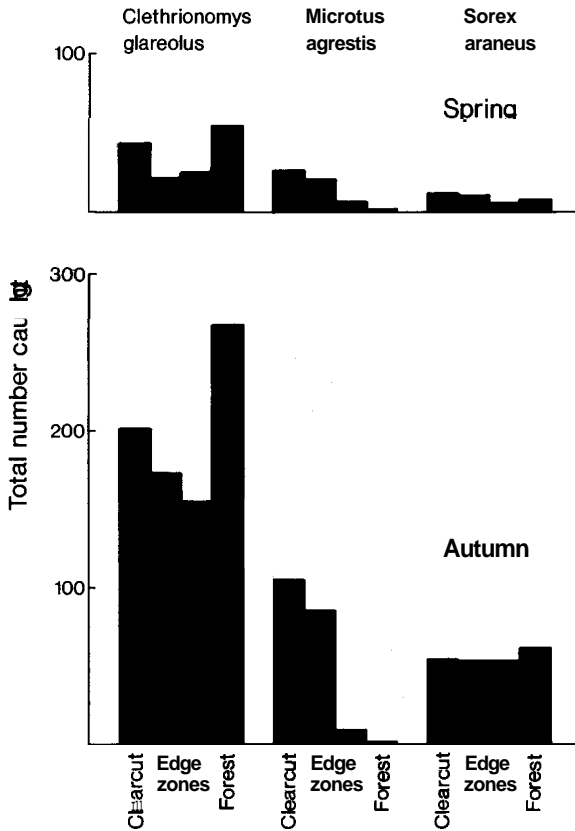


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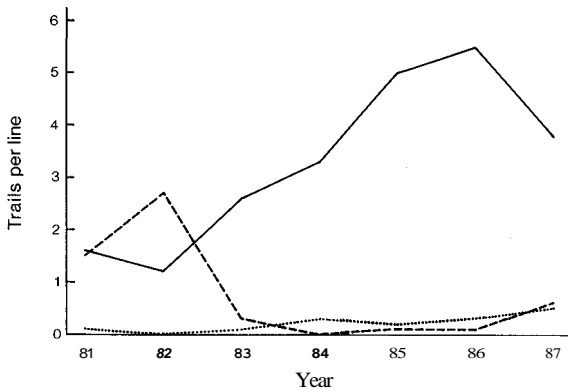


Fig. 3. Annual variations in trail numbers of three middle-sized mammal species, constituting a subcommunity in the forest landscape. Years refer to December of the tracking periods.

--- = fox *Vulpes vulpes*
 = marten *Martes martes*
 — = mountain hare *Lepus timidus*

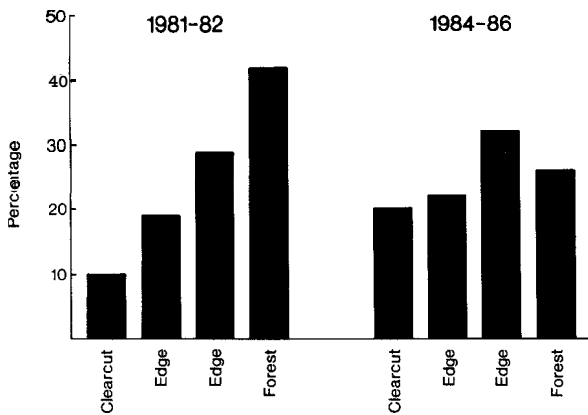


Fig. 4. Hare *Lepus timidus* distributions at high (1981–82) and low (1984–86) fox *Vulpes vulpes* numbers. Clearcut and forest sections denoted according to Fig. 1.

mobile and to move in exposed situations. The fox showed a steep decline in 1982–83 and an apparent recovery in 1986–87. During the absence of the fox, hare and marten tracks increased considerably and slightly, respectively (Fig. 3). Therefore, distributions of hare and marten trails during 1980–82 (for marten also during 1980–83 and 1987) were compared with corresponding numbers in 1984–86. There was a significant difference for hares (Fig. 4, $X^2 = 162.09, p < 0.001$) but not for the marten ($X^2 = 0.37, NS$). The hare trails were more common on clearcuts and edge parts of the forests

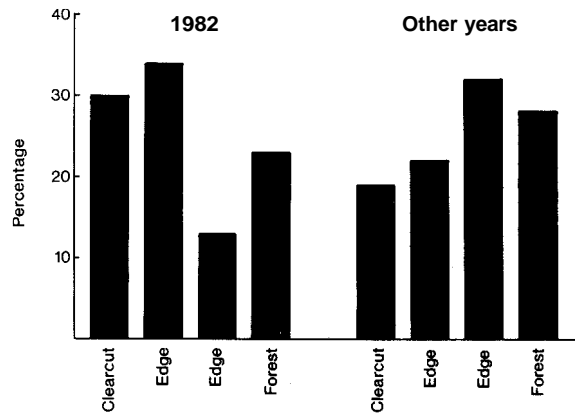


Fig. 5. Fox *Vulpes vulpes* distributions at high (1982) and low-intermediate (other years) abundance of the field vole *Microtus agrestis*. Clearcut and forest sections denoted according to Fig. 1.

Table 3A. Total distribution of observations of the most common bird species in spring 1980–92.

Species	Clearcut		Forest	
	Central	Edge	Edge	Interior
<i>Anthus trivialis</i>	79	134	62	61
<i>Prunella modularis</i>	19	20	40	20
<i>Erithacus rubecula</i>	68	78	339	261
<i>Saxicola rubetra</i>	30	3	0	0
<i>Turdus merula</i>	8	9	63	34
<i>Turdus philomelos</i>	11	8	97	79
<i>Turdus iliacus</i>	5	10	32	14
<i>Sylvia atricapilla</i>	4	9	8	15
<i>Phylloscopus trochilus</i>	79	66	213	152
<i>Regulus regulus</i>	1	0	120	91
<i>Ficedula hypoleuca</i>	5	2	21	17
<i>Parus montanus</i>	3	3	21	18
<i>Parus cristatus</i>	0	0	32	36
<i>Parus ater</i>	2	1	40	47
<i>Parus major</i>	24	41	43	23
<i>Lanius collurio</i>	9	2	0	0
<i>Fringilla coelebs</i>	23	21	769	569
<i>Carduelis spinus</i>	0	8	40	19
<i>Emberiza citrinella</i>	235	160	9	2

during the absence of the fox.

Peak rodent densities occurred in 1982–83 (mainly *M. agrestis*) and 1983–84 (mainly *C. glareolus*). Other peak rodent years, then mainly dominated by bank voles, appeared in 1987–89 and 1990–92. The field vole was largely restricted to

Table 3B. Spring distribution of bird species according to numerical dominance in various sections of the clearcut-forest gradient. For further explanations, see Table 2B.

Differences between habitats	Species	Differences within habitats	Species
Clearcut	<i>Anthus trivialis</i> < 0.001	Central clearcut	<i>Saxicola rubetra</i> < 0.001 <i>Emberiza citrinella</i> < 0.01 <i>Lanius collurio</i> < 0.05
		Clearcut edge	<i>Parus major</i> < 0.05
Forest	<i>Turdus philomelos</i> < 0.001 <i>Parus ater</i> < 0.001 <i>Parus cristatus</i> < 0.001 <i>Ficedula hypoleuca</i> < 0.001 <i>Parus montanus</i> < 0.001	Forest edge	<i>Fringilla coelebs</i> < 0.001 <i>Phylloscopus trochilus</i> < 0.01 <i>Turdus merula</i> < 0.01 <i>Erithacus rubecula</i> < 0.01 <i>Carduelis spinus</i> < 0.01 <i>Turdus illiacus</i> < 0.01 <i>Prunella modularis</i> < 0.01 <i>Regulus regulus</i> < 0.05

clearcuts and possible effects of peak *M. agrestis* numbers were examined on the distribution of its main predators. There was a significantly increased use of clearcuts by the fox during 1982–83 (Fig. 5, $X^2 = 27.96$, $p < 0.001$). Too few trails were available of the marten in 1982–83 for closer analyses, while ermines and least weasels did not show any evidence of habitat changes, or intra-clearcut changes, during the field vole year.

The total number of moose and roe deer trails per line and year were significantly negatively related ($r = -0.42$, $p = 0.01$). Therefore, the distribution of moose and roe deer trails were compared with the mean snow depth during the December–March period according to weather reports from the official meteorological station at Uppsala. The proportion of deer trails observed on clearcuts of each census line for both species were negatively related to mean snow depth but not significantly so. There were also insignificant positive relations between

snow and the number of both species at the forest edge. The negative interspecific relations were probably due to different long-distance movements in relation to food sources (feeding trays for roe deer and pine plantations with shallow snow for the moose).

3.4. Birds

About 50 bird species were observed during the 13 years of census but only 19 species (Table 3) were so common that statistical analyses were possible. Only the tree pipit (*A. trivialis*) showed especially high numbers at the very edge but most observations of this species were when singing in the air. The species composition on the clearcuts changed during the study period. Certain species typical of open ground (e.g. *S. rubetra* and *L. collurio*) more or less disappeared towards the end of the study,

Table 4A. Total distribution of observations of the most common bird species in late summer 1980–81 and 1988–89.

Species	Clearcut		Forest	
	Central	Edge	Edge	Interior
<i>Anthus trivialis</i>	7	13	9	3
<i>Erithacus rubecula</i>	3	7	46	27
<i>Turdus merula</i>	3	7	16	9
<i>Turdus philomelos</i>	11	11	27	18
<i>Phylloscopus trochilus</i>	6	13	31	18
<i>Regulus regulus</i>	1	0	54	39
<i>Parus montanus</i>	8	5	30	15
<i>Parus cristatus</i>	1	3	22	14
<i>Parus major</i>	9	20	8	6
<i>Lanius collurio</i>	41	14	0	0
<i>Fringilla coelebs</i>	2	9	23	19
<i>Emberiza citrinella</i>	21	9	0	0

while other species such as *P. trochilus* colonized the clearcuts. These successional changes will be analysed in another context.

In spring, three species (*S. rubetru*, *E. citrinellu* and *L. collurio*) showed a pronounced to clear preference for central parts of the clearcuts (Table 3B) while only one species (*A. trivialis*) preferred the clearcut parts closest to the forest. The great tit *P. major* showed a peak in occurrence extending over both the clearcut and the forest edge zones. Among the remaining thirteen species that were examined in greater detail and that preferred forest to clearcut, eight species occurred in largest numbers in the edge zone of the forest. Observations of only five species were equally divided between edge and interior parts of the forest and none preferred the interior forest. The edge effect was most pronounced in the chaffinch *F. coelebs*, possibly partly due to the general dominance in numbers by this species. However, all four of the most common forest species (*F. coelebs*, the willow warbler *Ph. trochilus*, the European robin *E. rubeculu* and the goldcrest *R. regulus*) showed a preference for forest edges. Two out of three thrush (*Turdus*) species showed an edge effect of this kind while none out of three typical coniferous forest titmice (*Parus*) species preferred the edge.

In summer, species differences between clearcuts and forests were generally the same as in spring

(Tables 4A and B). However, *A. trivialis* did not show any preference for forests or clearcuts at this season. *E. citrinellu* and *L. collurio* occurred significantly more often in central than in edge parts of the clearcuts while the clearcut distribution of *P. major* was the opposite. *E. rubeculu* and *P. montanus* were significantly more often seen in the edge than in the interior parts of the forest. All other species observed in reasonable numbers did not discriminate between habitat subdivisions.

4. Discussion

The vertebrate faunas of mature forests and clearcuts differed considerably. Certain species, such as *M. ugrestitis*, *M. ermineu* and *M. nivalis*, *E. citrinella*, *L. collurio* and *S. rubetru* were almost only observed on clearcuts. Fewer forest species were habitat limited but *S. vulgaris* was never observed and *S. minutus*, *R. regulus* and some conifer forest tits (*Purus* spp.) were very rarely observed on clearcuts. The typical clearcut species are not restricted to the taiga biome but are often equally common, or more common, in subarctic and temperate regions. Thus, they have not evolved to exploit disturbance patches within the taiga specifically but have likely immigrated from other and possibly ancient biomes. *M. ugrestitis* seems to have evolved as a species on tundra-steppe environments during interglacial periods (Nadachowski 1991) and its main predators, such as weasels (Henttonen 1987), may have survived glaciation in the tundra-steppe regions that bordered glaciated areas (Nilsson 1972). The typical birds on clearcuts may have come from biomes in early seral stages. All three clearcut specialists among the birds left the boreal forest in winter (*E. citrinella*, however, only for short distances), indicating that winter requirements are not met in this biome.

Coniferous forest bird species in central Sweden belong to a more generalized West European bird fauna than those in north Fennoscandian and north Russian forests, which include certain Siberian elements (Haila *et al.* 1987). Most of the forest species examined in this study showed great flexibility in habitat selection, a feature characteristic of most

Table 4B. Summer distribution of bird species according to numerical dominance in various sections of the clearcut-forest gradient. For further explanations, see Table 2B.

Differences between habitats	Species	Differences within habitats	Species
Clearcut		Central clearcut	<i>Lanius collurio</i> < 0.001 <i>Emberiza citrinella</i> < 0.05
		Clearcut edge	<i>Parus major</i> < 0.05
Forest	<i>Regulus regulus</i> < 0.001	Forest edge	<i>Parus montanus</i> < 0.05
	<i>Parus cristatus</i> < 0.001		<i>Erithacus rubecula</i> < 0.05
	<i>Fringilla coelebs</i> < 0.001		
	<i>Phylloscopus trochilus</i> < 0.001		
	<i>Turdus philomelos</i> < 0.05		
	<i>Turdus merula</i> < 0.05		

species at high latitudes (Stevens 1989; Pagel *et al.* 1991). It has even been argued that the specialized (Siberian?) species were purged from south and central Scandinavia by forest fragmentation already several hundred years ago (Angelstam 1992).

One important finding was the pronounced attraction of the forest edge zone to passerine birds in particular but also to some mammals such as *A. sylvaticus* and *C. capreolus*. Such an edge effect has been observed earlier in passerine birds (Hansson 1983; Helle 1984). Instead, hardly any of the examined species preferred the forest interior. This is in striking contrast to conditions in North American deciduous forests where many bird species avoid forest edges (*e.g.* Temple and Cary 1988). Many deciduous forest species seem to be interior specialists while generalistic birds prefer edges (Kroodsmma 1982; Lemkuhl *et al.* 1991). The specialist passerines are becoming rare or disappearing in fragmented North-East US deciduous forests while they are still common and obviously not affected by edge effects in mixed extensive forests in Ontario (Welsh 1987). The matrix consists of agricultural areas in North-East US and forest regeneration areas in Ontario. The American contrasts ap-

pear similar to the European situation and may be generally explained by the regional abundance of the specialist species, the latter being less affected in areas where the forest is still only moderately fragmented and only recently managed (Temple and Cary 1988).

The factors attracting birds to conifer forest edges are poorly understood. Luxuriant deciduous trees and shrubs develop at sunny edges (Helle 1984) and seem to support a richer invertebrate fauna than more pure and dark conifer forests (Helle and Muona 1985). Passerines such as the chaffinch move over much larger areas than defended by song (Hanski and Haila 1988). Forest edges may possibly be disproportionally used as song post but in such cases the trees at the very edge are obviously not preferred. However, the less pronounced use of forest edges in summer than in spring may indicate that the edge effect is related to territorial behaviour. The pronounced winter occurrences of the relatively small roe deer at forest edges is probably due to less snow than on the clearcuts. The clearcuts provide abundant food for ungulates (Moen 1973) and the clearcuts can easily be reached from the forest edges. However, the