Ann. Zool. Fennici 44: 486–495 ISSN 0003-455X (print), ISSN 1797-2450 (online)
Helsinki 19 December 2007

Seed crops of Norway spruce and winter habitat quality for boreal birds: old-growth compared with managed forests

Kjell Sjöberg, Roger B. Pettersson, John P. Ball* & Thomas Sundström

*Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden (*correspondig author's e-mail: John.Ball@vfm.slu.se)*

Received 16 Apr. 2006, revised version received 31 Oct. 2007, accepted 10 June 2006

Sjöberg, K., Pettersson, R. B., Ball, J. P. & Sundström, T. 2007: Seed crops of Norway spruce and winter habitat quality for boreal birds: old-growth compared with managed forests. — *Ann. Zool. Fennici* 44: 486–495.

We compared the winter bird community in 5 old-growth coniferous forests and adjacent managed forests in northern Sweden. Norway spruce seeds on snow (available to birds) were sampled during late winter and differed about 13-fold between 1990 and 1992. There were no significant differences between the old-growth and managed forest in the seed-rich (mast) year, but during the seed-poor (normal) year there were more birds in total, and more birds belonging to the biogeographical group *Northern taiga species* in the old-growth forests. Our analysis suggests that differences in habitat quality between old-growth and managed forests may be small in the rare years with high spruce seed production, but in an average year, old-growth forests seem to be better for wintering birds. This pattern, although needing further study to determine its generality, is consistent with suggestions that forestry may negatively influence the avian community by reducing winter habitat quality.

Introduction

In the taiga region, some birds are sedentary and live in the boreal forest throughout the winter. Data from northern Finland suggests that these year-round residents of the taiga may be particularly vulnerable to forestry, especially when it results in fragmentation of old-growth forests or a change in forest age structure (Järvinen *et al.* 1977, Helle & Järvinen 1986, Virkkala 1987a). In Finland, there has been a decrease in the number of birds belonging to the "Northern taiga" bird group during recent decades (Siberian jay *Perisoreus infaustus*, Siberian tit *Parus cinctus*, pine grosbeak *Pinicola enucleator,* capercaillie *Tetrao urogallus*, three-toed woodpecker *Picoides tridactylus*; Järvinen & Väisänen 1978, 1979, Helle 1984, Helle & Järvinen 1986, Virkkala 1987b, Brotons *et al.* 2003). In Sweden, forestry practices are rather similar to those in Finland, so one may expect the same general negative impacts on bird communities. For example, Svensson *et al.* (1992) found negative trends particularly in bird species living in the "old-growth" forest type. Furthermore, Edenius and Elmberg (1996) found negative effects on the abundance of breeding species by large-scale clear-cutting forestry in a study in northern Sweden.

However, not much is actually known about the effect on birds of forestry activities in the old-growth forest habitats of northern Scandinavia during winter even though the Northern taiga region is one where we might expect modern forestry to exert a strong influence. Winter conditions ought to be of particular importance for sedentary birds, and these winter conditions may help explain the downward trends in many of these breeding birds. Here, we compare the bird communities in old-growth to managed forests during winter. Because we expect different functional and/or biogeographic groups of birds (e.g. seed specialists, hoarding birds, Northern taiga birds) to be differentially affected by forestry, we consider them separately.

The sporadic pulsing of resources (like the periodic mast production by trees that is often attributed to having evolved in an attempt to swamp consumers; e.g. Fenner 1991) happens in many terrestrial ecosystems and is being increasingly considered in understanding consumer dynamics (e.g. Jensen 1982, Ostfeld & Keesing 2000, Satake & Bjornstad 2004, Koenig & Liebhold 2005). Our study included two years which were extremely different in spruce seed production, so we were able to contribute to this growing body of literature that considers pulsed resources by comparing the avian communities between old-growth and managed forests in both a year with very high and a normal (i.e. low) availability of seeds. We predicted that, in years of super-abundant seed production (i.e. high mast production), old-growth and managed forests may be similar as winter habitat, but differ in years of low (i.e. normal) seed abundance.

Material and methods

Study area

We selected five old-growth forests in the Middle and Northern Boreal Zones (Ahti *et al.* 1968) of northern Sweden. To reduce heterogeneity among sites and improve the statistical power of our tests, the following criteria were applied to select areas for study: (i) located in an inland within the Middle or Northern Boreal Zone (but excluding the forests bordering the Scandinavian mountain range), (ii) surrounded by managed forest landscapes, (iii) dominated by old-growth spruce forest (with *Alectoria sarmentosa* as the most characteristic epiphytic lichen), and (iv) with an altitude of 375–520 m. This resulted in the selection of five large forest reserves in Sweden: Luottåive (66°22´N, 20°00´E) in the county of Norrbotten, Alpliden (64°41´N, 17°38´E) and Stenbithöjden (64°01´N, 16°57´E) in the county of Västerbotten, and Kålhuvudet (63°38´N, 18°28´E) and Jämtgaveln (62°41´N, 15°55´E) in the county of Västernorrland (Fig. 1). These areas range in size from 200 to 1500 ha.

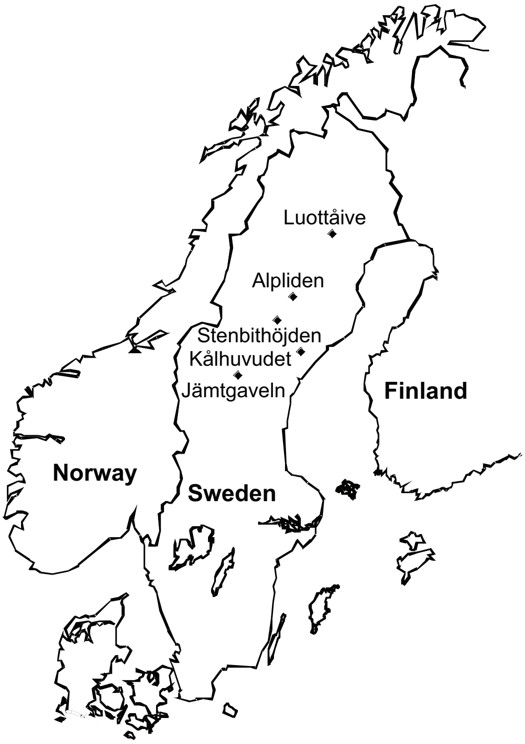

Fig. 1. Map of Sweden showing the five study areas, each with both old-growth and managed forests.

To guard against confounding, we used a paired design in which we selected a managed forest stand with a minimum area of 50 ha within 10 km from each of the old-growth forest reserves. The managed stands consisted of mature (ca. 100 years old) spruce forest that had been selectively cut or thinned on one or more occasions. Old-growth and managed stands had a similar vegetation composition with *Vaccinium myrtillus* as the dominant ground vegetation.

In an area of 2 ha within each site, forest stands were evaluated in greater detail. The old-growth forests were significantly older than the managed forests (186 and 102 years, respectively; Wilcoxon signed ranks test: $z = 2.51$, $p = 0.01$), but the mean basal tree area did not differ significantly (28 and 33 $m^2\ ha^{-1}$ respectively; Wilcoxon signed ranks test: $z = 1.46$, $p = 0.14$). However, it should be noted that unlike many managed forests in Scandinavia, our managed forests were not planted by man and are thus more likely to resemble old-growth forests. They were all naturally-regenerated forests, but have been harvested to some extent; for example there has been some dimension or single-tree selective felling. Furthermore, these are not highly-managed and homogenous coniferous forests — in a few areas deciduous trees are scattered among the coniferous stands, especially along water courses. Snow normally covers the ground within the study areas until May. For further details about the study area, *see* Pettersson *et al.* (1995), and Esseen *et al.* (1996).

The bird community was investigated in each of the five ca. 50-ha-sites by skiing along transect lines (100 m apart) during 28 February–4 April 1990, and 3–26 March 1992. The line transect method was used (Koskimies & Väisänen 1991), i.e. all observations of birds within ca. 50 m of each side of a five km line were noted. A single observer conducted all censuses to eliminate any variation among observers. Because we did not test for 100% detectability at the extreme edges of this 50-m transect, we decided to take the conservative step of treating the avian data as an index, rather than calculating absolute density. The use of an index rather than an estimate of absolute density does not, of course, affect our ability to contrast the paired data from the old growth forest and the managed forest.

The bird censuses started in the morning and each 5-km transect took 3–4 hours. The weather conditions were similar for all surveys and no surveys were performed during days with strong wind or snowfall. The temperature normally fluctuated around 0 °C during the surveys, although the extremes ranged from –20 to +5 °C. We started the field work in the southernmost site, and ended in the northernmost one, to make the surveys more equal from a phenological point of view.

Occasional observations of birds flying over the forests, such as whooper swan (*Cygnus cygnus*) and snow bunting (*Plectrophenax nivalis*), were excluded from the observation list. As some birds were sedentary, while other were migratory or temporary visitors, in the analyses bird species were divided into different functional groups. Because the abundance of spruce seeds differed between years, and because some birds are known to be specialised seed-eaters (e.g. the crossbill (*Loxia curvirostra*), siskin (*Carduelis spinus*) and redpoll (*C. flammea*), we consider these seed specialists as a group. Other functional and biogeographic species groups are hoarding birds, Southern and Northern taiga bird species (*see* Table 1). The “Northern taiga species group” is based on previous work by Järvinen and Väisänen (1979), Väisänen *et al.* (1986), Helle and Järvinen (1986), and Virkkala (1987b, 1991a, 1991b), but note that the name reflects “typical” habitat, and is not meant to suggest that these birds are exclusive to such areas.

At the same time as the line transect was conducted, spruce seeds were counted in ten randomly selected 1 × 1 m^2 sampling plots on the snow surface at each of the five (paired) sites. Although several plants in our study area are known to exhibit variable seed production (e.g. birch *Betula* spp., rowan *Sorbus aucuparia*, bilberry *Vaccinium myrtillus)*, few of these species were available to birds when we conducted our study in late winter (e.g. because of species-specific timing of seed release, or burial under snow). Furthermore, our study areas were heavily dominated by spruce. Thus, while we cannot rule out influences of variation in seed abundances of other plants, they are unlikely to strongly influence our conclusions regarding spruce-dominated forests.

Regarding statistical analysis, residual analysis (Tabachnick & Fidell 1983) indicated that the assumptions of parametric analyses (e.g. ANOVA) were not met, and could not be corrected fully by transformations. Given that our sample sizes were not large, we therefore took a conservative approach and used the Wilcoxon Signed-Ranks test, a common but powerful non-parametric statistical analysis because it is robust at these sample sizes (Siegel & Castellan 1988).

Because some bird species belonged to more than one functional or biogeographic group, we applied the Bonferroni correction (e.g. Iles 1999) to control for this aspect and ensure a more conservative analysis. All tests were performed with SAS (SAS Institute Inc. 1989).

Table 1. Mean number of birds per 5 km of transect sampled at 5 paired study areas (each > 50 ha, and each with an old-growth and a managed forest) ± 1 SE. SP: seed specialists, HS: hoarding species, ST: Southern taiga species, NT: Northern taiga species. Note that a species may belong to more than one functional or biogeographical group.

	High seed year		Low seed year	
	Old-growth forest	Managed forest	Old-growth forest	Managed forest
Seed eaters				
Great Spotted woodpecker (*Dendrocopos major* L.) ST	0.2 ± 0.2	0.6 ± 0.3	0.0 ± 0.0	0.2 ± 0.2
Siberian jay (*Perisoreus infaustus* L.) HS, NT	2.2 ± 0.5	3.0 ± 1.4	4.2 ± 1.4	3.0 ± 1.0
Goldcrest (*Regulus regulus* L.) ST	6.8 ± 3.4	8.2 ± 5.2	1.2 ± 0.5	1.6 ± 0.5
Willow tit (*Parus montanus* Conrad) HS	18.6 ± 3.5	20.0 ± 6.0	7.6 ± 1.7	5.8 ± 2.3
Siberian tit (*Parus cinctus* Boddaert) HS, NT	1.2 ± 0.8	0.4 ± 0.4	2.8 ± 2.6	0.0 ± 0.0
Coal tit (*Parus ater* L.) HS, ST	6.6 ± 3.4	4.8 ± 3.1	1.4 ± 0.3	2.4 ± 0.5
Great tit (*Parus major* L.) ST	0.4 ± 0.4	1.6 ± 0.7	0.2 ± 0.2	0.4 ± 0.3
Tree creeper (*Certhia familiaris* L.) ST	3.0 ± 0.9	1.8 ± 1.1	1.0 ± 0.5	2.6 ± 1.1
Chaffinch (*Fringilla coelebs* L.) ST	1.2 ± 1.2	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
Bullfinch (*Pyrrhula pyrrhula* L.) ST	2.8 ± 1.2	3.2 ± 1.2	2.4 ± 1.2	1.0 ± 0.6
Siskin (*Carduelis spinus* L.) SP, ST	7.4 ± 0.9	8.6 ± 2.7	0.0 ± 0.0	0.0 ± 0.0
Redpoll (*Carduelis flammea* L.) SP	39.0 ± 26.1	61.0 ± 30.2	4.2 ± 0.7	3.4 ± 1.4
Arctic redpoll (*Carduelis hornemanni* Holboell) SP	1.6 ± 1.2	1.2 ± 1.2	1.2 ± 1.2	0.0 ± 0.0
Pine grosbeak (*Pinicola enucleator* L.) NT	12.6 ± 4.4	11.0 ± 8.8	9.2 ± 2.2	1.2 ± 0.8
Crossbill (*Loxia curvirostra* L.) SP	18.0 ± 8.6	23.4 ± 7.1	3.8 ± 2.2	1.2 ± 0.5
Parrot crossbill (*Loxia pytyopsittacus* Borkhausen) SP	0.6 ± 0.4	2.4 ± 2.2	0.0 ± 0.0	0.0 ± 0.0
Two-barred crossbill (*Loxia leucoptera* Gmelin) SP	0.2 ± 0.2	0.4 ± 0.4	2.0 ± 2.0	0.0 ± 0.0
Crossbills (*Loxia* spp.) SP	9.2 ± 5.7	9.2 ± 4.2	0.0 ± 0.0	0.0 ± 0.0
Yellowhammer (*Emberiza citrinella* L.)	0.2 ± 0.2	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
Subtotal	131.8 ± 36.1	161.2 ± 42.1	41.2 ± 9.4	22.8 ± 5.2
Woodland grouse				
Willow grouse (*Lagopus lagopus* L.)	2.2 ± 1.4	0.8 ± 0.5	0.8 ± 0.5	0.0 ± 0.0
Capercaillie (*Tetrao urogallus* L.) NT	0.8 ± 0.2	1.2 ± 0.6	1.0 ± 0.5	0.6 ± 0.4
Black grouse (*Tetrao tetrix* L.)	2.2 ± 1.5	4.2 ± 1.9	0.4 ± 0.4	0.0 ± 0.0
Hazel hen (*Bonasa bonasia* L.)	1.2 ± 0.4	2.0 ± 0.5	1.8 ± 0.5	1.0 ± 0.6
Subtotal	6.4 ± 1.6	8.2 ± 2.0	4.0 ± 0.9	1.6 ± 0.5
Birds of prey				
Golden eagle (*Aquila chrysaetos* L.)	0.4 ± 0.4	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0
Goshawk (*Accipiter gentilis* L.)	0.2 ± 0.2	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0
Pygmy owl (*Glaucidium passerinum* L.)	0.8 ± 0.4	0.4 ± 0.3	0.4 ± 0.3	0.2 ± 0.2
Tengmalm's owl (*Aegolius funereus* L.)	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Hawk owl (*Surnia ulula* L.)	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0
Subtotal	1.6 ± 0.7	0.4 ± 0.3	1.0 ± 0.5	0.2 ± 0.2
Others				
Jay (*Garrulus glandarius* L.)	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
Hooded crow (*Corvus corone* L.)	0.0 ± 0.0	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0
Raven (*Corvus corax* L.)	2.4 ± 0.9	1.2 ± 0.4	2.0 ± 1.1	0.8 ± 0.5
Three-toed woodpecker (*Picoides tridactylus* L.) NT	2.0 ± 0.9	2.0 ± 0.7	2.0 ± 0.6	0.8 ± 0.2
Black woodpecker (*Dryocopus martius* L.)	0.0 ± 0.0	0.6 ± 0.4	0.2 ± 0.2	0.8 ± 0.6
Subtotal	4.4 ± 1.3	4.2 ± 0.7	4.2 ± 1.4	2.4 ± 0.5
Total	144.2 ± 37.0	174.0 ± 43.8	50.4 ± 10.9	27.0 ± 4.8

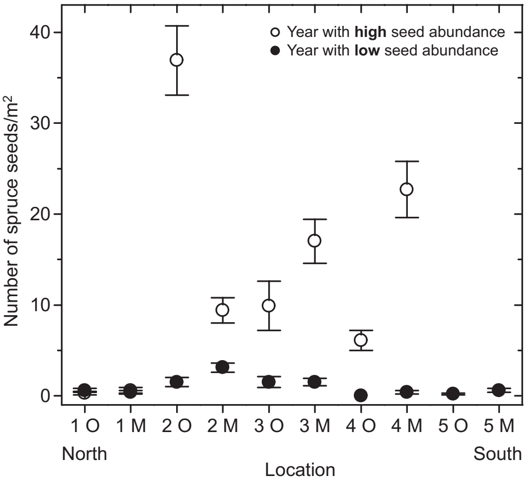

Fig. 2. Mean number ± 1 SE of spruce seeds per m^2 (n = 10 sample plots of 1 m^2 for each point) in old-growth (O) and managed (M) forests. Locations: 1 = Luottåive, 2 = Alpliden, 3 = Stenbitshöjden, 4 = Kålhuvudet, 5 = Jämtgaveln. Seeds were not counted at location 5 in 1990.

Results

Seed abundance

Between years, the mean number of seeds on the snow surface differed by a factor of almost 13 (12.9 *vs.* 1.0 seeds/m^2; Wilcoxon signed ranks test: $z = 2.37$, $p = 0.02$, Fig. 2). The unusually high seed production in 1990 was also recorded by Hofgaard (1993) who observed almost five times more spruce seeds in 1990 than in 1992 in a high altitude old-growth spruce forest in northern Sweden. Furthermore, this pattern held over large geographic areas: in northern Sweden, the abundance of spruce cones between the latitudes 56°–68° and altitudes 100–700 m was much higher in 1990 than in 1992 (Lestander & Wennström 1991, Wennström 1991).

Patterns of bird abundance

In comparing old-growth and managed forests during the seed-rich year, there were no significant differences in numbers of bird species (Fig. 3A), in total number of birds (Fig. 3B) or in any of the functional or biogeographic groups of birds measured (i.e. seed specialists (Fig. 3C), hoarding birds (Fig. 3D), Northern taiga birds (Fig. 3E), or Southern taiga birds (Fig. 3F) (Wilcoxon Signed-Ranks test: $p > 0.28$ for all).

In the seed-poor year, there were no significant differences between old growth forests and managed forests in the number of bird species (Fig. 3A), total number of birds (Fig. 3B), seed specialists (Fig. 3C), hoarding birds (Fig. 3D), or Southern taiga birds (Fig. 3F) (Wilcoxon Signed-Ranks test: $p > 0.18$ for all). However, there was significantly more of the birds of the Northern taiga group in old-growth than in managed forests (Wilcoxon Signed-Ranks test: $z = 2.52$, $p < 0.05$ after Bonferroni correction, Fig. 3E).

Turning now to a comparison of the seed-rich year to the seed-poor year to evaluate the potential role of a year with high spruce seed production (i.e. a "mast year") on the avian community in the area (rather than to compare managed to old-growth forests), we find that there were significant differences in numbers of bird species ($p < 0.01$, Fig. 3A), in total number of birds ($p < 0.001$, Fig. 3B) and in the biogeographic group Southern taiga species ($p < 0.001$, Fig. 3F), but not for Northern taiga birds ($p > 0.20$, Fig. 3E). In all cases the numbers of birds were higher in the seed-rich year, and there were nearly three times as many birds in the old-growth forest and more than six times as many birds in the managed stands, compared with the seed-poor year (Table 1 and Fig. 3B).

Discussion

Patterns of bird abundance

Firstly, there were large differences in overall bird abundance between the seed-rich year and the seed-poor year: nearly three times as many birds in the old-growth forests during the seed-rich year than in the seed-poor year (Table 1 and Fig. 3B). The difference between years was even more pronounced in the managed forest, which had more than six times as many birds during the high seed year. This suggests that (even assessed with such a simple metric as total bird numbers as a first step), periodic fluctuations in spruce mast may influence the general winter bird community, and that any such effect may be more

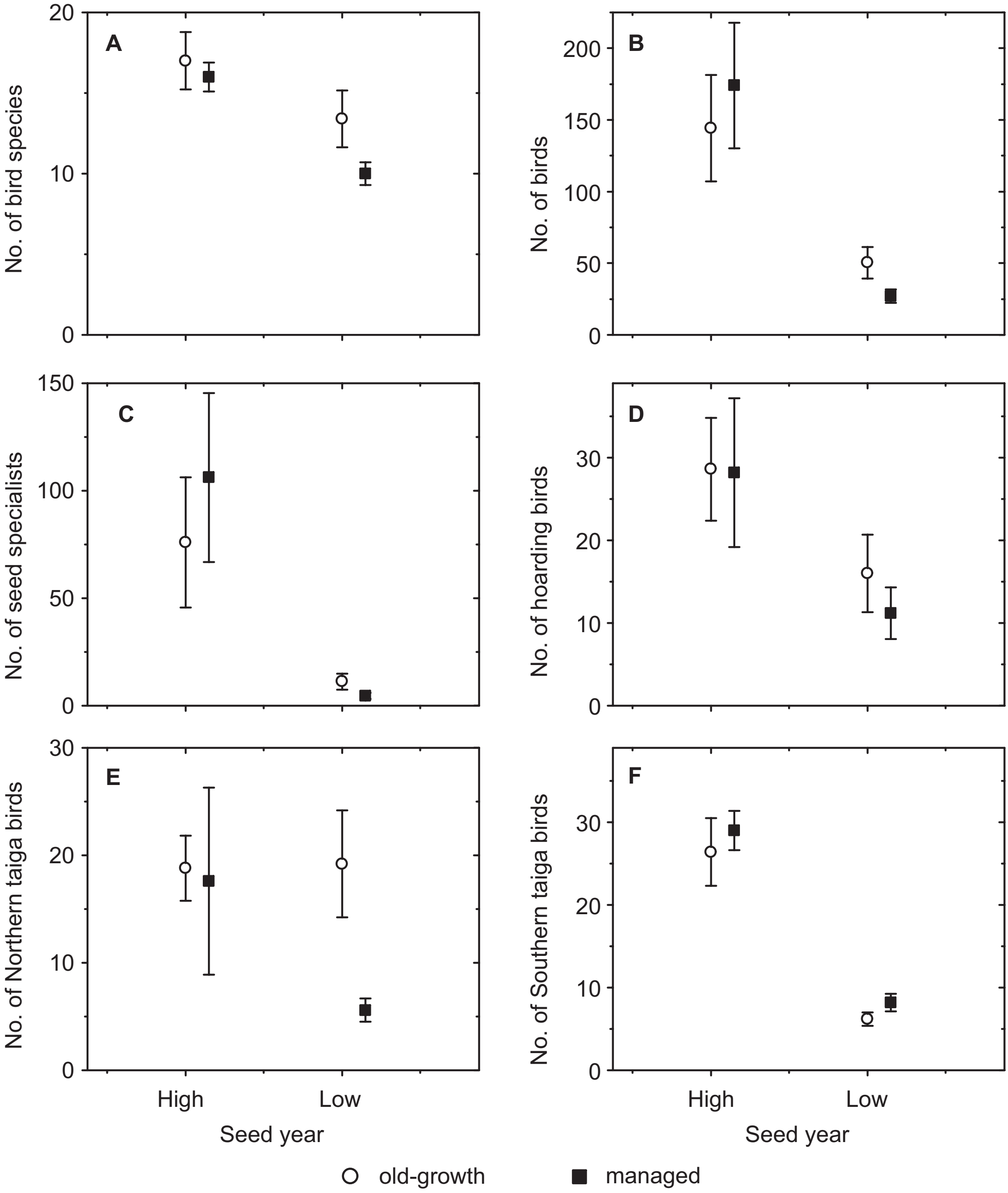

Fig. 3. Mean number ± 1 SE of (**A**) bird species, (**B**) birds, (**C**) seed specialists, (**D**) hoarding birds, (**E**) Northern taiga birds, and (**F**) Southern taiga birds (*n* = 5 pairs of old-growth and managed forests).

pronounced in managed forests, with quality of old growth forests being less variable among years.

Secondly, there were statistically-significant differences in the abundance of the biogeographic group Northern taiga species between the old-growth and managed forest types (Fig. 3E), but it is important to note that this difference was only in the seed-poor year (i.e. a "normal" year) and not in the seed-rich ("mast") year (Fig. 3E). Perhaps more strikingly, the numbers of Northern taiga birds was stable between "high" and "low" mast years in the old growth forests, but declined dramatically (Fig. 3E) from the "high" mast year to the "low" (i.e. normal, "non-mast") year in managed forests. Taken together, these observations suggest that the old-growth forests may provide better habitat than even rather old stands within managed forests in such (normal) seed-poor years.

During winter, old growth forests may provide superior habitat for insectivorous passerines because lichens are more abundant in the old trees which provides more and better substrates for the invertebrates consumed by these birds, and in which hoarding passerines cache their invertebrate prey (e.g. Pettersson *et al.* 1995, Esseen *et al.* 1996). Furthermore (and more directly relevant to our study), hoarding passerines use lichens to cache seeds and berries as well, so the greater abundance of lichens in old-growth forests may contribute to these areas being better winter habitat by providing both more food, and more opportunities for hoarding both seeds (including spruce seeds) and invertebrate prey (*see* Pettersson *et al.* 1995). For some of these species there is more specific knowledge about their autecology. For example, the Siberian tit, which is a hoarding bird species, prefers large forest areas with many dead trees and large coniferous trees. They avoid heavily thinned, open managed forests (possibly due to a lowered foraging efficiency in such habitats: Virkkala 1990, Virkkala & Liehu 1990).

The Northern taiga species, (capercaillie *Tetrao urogallus*, Siberian tit *Parus cinctus*, Siberian jay *Perisoreus infaustus*, pine grosbeak *Pinicola enucleator* and three-toed woodpecker), prefer virgin, old forests (Virkkala 1987b). They are all sedentary, and thus spend the winter in the area. The Siberian Jay, which also is a hoarding species, does not seem to be as habitat-specific as the Siberian tit (Table 1). Perhaps any potential differences between old growth and old managed forests (as in this survey) are not as important for populations of this sedentary species as is habitat loss or fragmentation (which of course are also effects of forestry).

Overall, comparing old-growth forests and managed forests, there were more birds in total, and more birds of the biogeographic group Northern taiga birds in the old-growth forests in the seed-poor year. Most importantly, however, the difference between the two years seems to be mainly decreased abundance of Northern taiga birds in the managed forests during the seed-poor year, suggesting that for this group of birds, the benefits of retaining old-growth forests may be particularly evident during years with limited (i.e. "normal") food abundance. This is consistent with the hypothesis that modern forestry practices may be contributing to the decline of these birds by reducing the quality of their habitats during winter. Of course, our study is observational and not experimental, so some bird species may have been responding to factors other than changes in spruce seed density even though the paired study design should effectively block any such confounding.

It ought to be stressed that the differences we detected between the old-growth and managed forests were in spite of the fact that our managed forests were not planted by humans, were quite old (near maturity and ready for harvest), were comparatively little affected by forestry activities, and thus still resembled old-growth forests in many respects. We suggest that the differences between managed forests and old-growth forests for boreal birds might be even more pronounced if our managed forests had been the more homogenous type planted by man, or were younger. Thus, our results might be conservative estimates of the differences in bird communities between old-growth and "average" managed forests in late winter in Fennoscandia, and the magnitude of differences between old-growth and managed forests could be greater than our analysis reveals.

Seeds of coniferous trees are an important part of the diet for many bird species. The willow tit, for example, stores seeds most of the year if seeds are available. This is the case also for the coal tit, crested tit (*P. cristatus*) and Siberian tit (Haftorn 1953, 1956a, 1956b). In a study of hoarding behaviour carried out in March in a seed-rich year, Alatalo and Carlsson (1987) concluded that the food eaten and hoarded by willow and Siberian tits consisted almost exclusively of spruce seeds. Also, the Siberian Jay is known for its hoarding behaviour (e.g. Blomgren 1964). At least for these birds, seed availability might be important for winter survival. That many species of forest trees exhibit low seed production most years, and only rarely show high seed production, has been noted (e.g. Fenner 1991). Although this phenomenon has other explanations (e.g. good growing weather being rare), a common explanation for this variation is the "predator saturation hypothesis" (Fenner 1991). In brief, the irregular production of seeds may be an evolutionary strategy adopted by some tree species to starve out their seed predators in years with low production of seeds, and then overwhelm them with high production in other years. Regardless of the underlying cause, spruce in our area only rarely exhibits the abundant seed production we observed in our "high" year — most years are like our "low" year.

In a 12-year study of breeding passerine birds in spruce-dominated forests in central Norway, Hogstad (1993) documented considerable variation in bird density between years, suggesting species-specific influences by different factors (and seasonal differences as well). For example, siskin population density varied from two to eight territories per km^2. The variation was closely related to the abundance of spruce seeds, but not to the abundance of pine seeds (cone crops of spruce and pine varied considerably during the study period, but not synchronously). Similarly, Summers (1999) documented numerical responses by crossbills *Loxia* spp. to annual fluctuations in cone crops, and more recently Virkkala (2004) reported similar numerical fluctuations in the numbers of crossbills and siskins with spruce cone crops in southern boreal forests.

We do not suggest that spruce seed crops are the only factor influencing the avian community during winter and which varies among years. For example, for a good seed-year in spruce, it must have been a warm summer the year before. Perhaps this is a good situation for forest birds in general, including the woodland grouse species. This could affect both the survival of the chicks, as well as food availability for the adults. There might also be a generally relaxed predator pressure as an indirect effect of high seed availability. For example, a higher population of seed-eating mammals (e.g. squirrels and mice) might lower the pressure from raptors on grouse species. Squirrels fluctuate in number from year to year, possibly in response to changes in seed abundance (Pulliainen 1973). In central Sweden, squirrels made up 64% of goshawk (*Accipiter gentilis*) prey during winter in a year with high density of squirrels (Widén 1987). In other years, woodland grouse (especially the hazel hen) made up the bulk of the diet of the goshawk during the winter in Finnish and Swedish studies (e.g. Sulkava 1964, Widén 1987). Abundant small mammals could have a similar buffering effect on predator pressure from the red fox (*Vulpes vulpes*; e.g. Lindström *et al.* 1994) and the marten (*Martes martes*; Nyholm 1970).

Conclusions

Birds have been intensively studied in northern Europe, but we do not know enough about many species to really understand their population regulation (Niemi *et al.* 1998). A large part of the decline in boreal birds is likely due to the impacts of forest destruction and fragmentation on breeding as others have suggested, but our analysis here suggests that forestry may also affect boreal birds in winter via a reduction in habitat quality. Specifically, in winters with low seed abundance (which happens most years), there were significantly more Northern taiga species in old growth forests (i.e. those never harvested) than in managed forests — even if these managed forests are quite old (and near harvest), as ours were. The pattern revealed by our analysis are thus consistent with suggestions that modern forestry practices may be contributing to the decline of many passerine birds by reducing the quality of their winter habitats in most years. Finally, because our managed forests were quite old, of natural origin and not of the uniform type often planted by modern forestry, the late winter superiority of old-growth forests as bird habitats as compared with managed forests may be even greater than our analysis revealed.

Acknowledgements

Karl-Erik Renhorn provided valuable field assistance. Funding was provided by the Centre of Environmental Research, Umeå. Comments by Mats Lindén, Lars Edenius, and particularly two anonymous reviewers improved the paper.

References

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. — *Ann. Bot. Fennici* 5:169–211.

Alatalo, R. V. & Carlson. A. 1987: Hoarding-site selection of the Willow Tit *Parus montanus* in the presence of the Siberian Tit *Parus cinctus*. — *Ornis Fennica* 64:1–9.

Blomgren, A. 1964: *Lavskrika*. — Bonniers, Stockholm.

Brotons, L., Mönkkönen, M., Huhta, E., Nikula, A. & Rajasarkka, A. 2003: Effects of landscape structure and forest reserve location on old-growth forest bird species in northern Finland. — *Landscape Ecology* 18: 377–393.

Edenius, L. & Elmberg, J. 1996: Landscape level effects of modern forestry on bird communities in North Swedish boreal forests. — *Landscape Ecology* 11: 325–338.

Esseen, P.-A., Renhorn, K.-E. & Pettersson, R. B. 1996: Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. — *Ecol. Appl.* 6: 228–238.

Fenner, M. 1991: Irregular seed crops in forest trees. — *Quarterly J. Forestry* 85: 166–172.

Haftorn, S. 1953: Observasjoner over hamstring av naering også hos lappmeis *Parus c. cinctus* Bodd. — *K. norske Vidensk. Selsk. Forh.* 26: 76–82.

Haftorn, S. 1956a: Contribution to the food biology of tits especially about storing of surplus food, Part II. The coal-tit (*Parus a. ater* L.). — *K. norske Vidensk. Selsk. Skr.* 1956: 1–52.

Haftorn, S. 1956b: Contribution to the food biology of tits especially about storing of surplus food, Part III. The willow-tit (*Parus atricapillus* L.). — *K. norske Vidensk. Selsk. Skr.* 1956: 1–79.

Helle, P. 1984: Effect of habitat area on breeding bird communities in northeastern Finland. — *Ann. Zool. Fennici* 21: 421–425.

Helle, P. & Järvinen, O. 1986: Population trends of North Finnish land birds in relation to their habitat selection and changes in forest structure. — *Oikos* 46: 107–115.

Hofgaard, A. 1993: Seed rain quantity and quality, 1984–1992, in a high altitude old-growth spruce forest, northern Sweden. — *New Phytol.* 125: 635–640.

Hogstad, O. 1993: Structure and dynamics of a passerine bird community in a spruce-dominated boreal forest. A 12-year study. — *Ann. Zool. Fennici* 30: 43–54.

Iles, T. C. 1999: Multiple regression. — In: Fry, J. C. (ed.), *Biological data analysis: a practical approach*: 127–172. Oxford University Press.

Jensen, T. S. 1982: Seed production and outbreaks of non-cyclic rodent populations in deciduous forests — *Oecologia* 54: 184–192.

Järvinen, O., Kuusela, K. & Väisänen, R. A. 1977: Effects of modern forestry on the numbers of breeding birds in Finland in 1945–1975. — *Silva Fennica* 11: 284–294. [In Finnish with English summary].

Järvinen, O. & Väisänen, R. A. 1978: Recent changes in forest bird populations in northern Finland. — *Ann. Zool. Fennici* 15: 279–289.

Järvinen, O. & Väisänen, R. A. 1979: Climatic changes, habitat changes, and competition: dynamics of geographical overlap in two pairs of congeneric bird species in Finland. — *Oikos* 33: 261–271.

Koenig, W. D. & Liebhold, A. M. 2005: Effects of periodical cicada emergences on abundance and synchrony of avian populations. — *Ecology* 86: 1873–1882.

Koskimies, P. & Väisänen, R. A. (eds.) 1991: *Monitoring bird populations*. — Finnish Museum of Natural History, Helsinki.

Lestander T. & Wennström, U. 1991: *Kottförekomst och frökvalitet insamlingssäsongen 1989/90*. — Inst. f. skogsförädling, Rapport nr. 1, 1989/90.

Lindström, E., Andrén, H., Angelstam, P. Cederlund, G., Hörnfeldt, B., Jäderberg, L., Lemnell, P.-A., Martinsson, B., Sköld, K. & Swenson, J. E. 1994: Disease reveals the predator: Sarcoptic mange, red fox predation, and prey populations. — *Ecology* 75: 1042–1049.

Niemi, G., Hanowski, J, Helle, P., Howe, R., Mönkkönen, M., Venier, L. & Welsh, D. 1998: Ecological sustainability of birds in boreal forests. — *Conservation Ecology* (online) 2(2): 1–17.

Nyholm, E. 1970: On the ecology of the pine marten in eastern and northern Finland. — *Suomen Riista* 22: 105–118. [In Finnish with English summary].

Ostfeld, R. S. & Keesing, F. 2000: Pulsed resources and community dynamics of consumers in terrestrial ecosystems. — *Trends Ecol. Evol.* 15: 232–237.

Pettersson, R. B., Ball, J. P., Renhorn, K.-E., Esseen, P.-A. & Sjöberg, K. 1995: Invertebrate communities in bor eal forest canopies as influenced by forestry and lichens with implications for passerine birds. — *Biol. Conserv.* 74: 57–63.

Pulliainen, E. 1973: Winter ecology of the red squirrel (*Sciurus vulgaris* L.) in northeastern Finland. — *Ann. Zool. Fennici* 10: 487–494.

SAS Institute Inc. 1989: *SAS/STAT user's guide, ver. 6.* — Cary, NC. SAS Institute Inc.

Satake, A. & Bjørnstad, O. N. 2004: Spatial dynamics of specialist seed predators on synchronized and intermittent seed production of host plants. — *Am. Nat.* 163: 591–605.

Siegel, S. & Castellan, N. J. 1988: *Nonparametric statistics for the behavioural sciences*. — McGraw-Hill.

Sulkava, S. 1964: Zur Nahrungsbilogie des Habichts, *Accipiter g. gentilis* (L.) *Aquilo*. — *Ser. Zool.* 3: 1–103.

Summers, R. W. 1999: Numerical responses by crossbills *Loxia* spp. to annual fluctuations in cone crops. — *Ornis Fennica* 76: 141–144.

Svensson, S., Olsson, O. & Svensson, M. 1992: *Förändringar i fågelfaunan. Beståndsprognoser och forskningsbehov för vissa arter — en litteraturstudie*. Naturvårdsverket Rapport 4095.

Tabachnick, B. G. & Fidell, L. S. 1983: *Using multivariate statistics*. — Harper and Row, New York, NY.

Virkkala, R. 1987a: Effects of forest management on birds breeding in northern Finland. — *Ann. Zool. Fennici* 24: 281–294.

Virkkala, R. 1987b: Geographical variation in bird communities of old, intact forests in northern Finland. — *Ornis Fennica* 64: 107–118.

Virkkala, R. 1990: Ecology of the Siberian tit *Parus cinctus* in relation to habitat quality: effects of forest management. — *Ornis Scand.* 21: 139–146.

Virkkala, R. 1991a: Spatial and temporal variation in bird communities and populations in north-boreal coniferous forests: a multiscale approach. — *Oikos* 62: 59–66.

Virkkala, R. 1991b: Population trends of forest birds in a Finnish lapland landscape of large habitat blocks: consequences of stochastic environmental variation or regional habitat alteration? — *Biol. Conserv.* 56: 223–240.

Virkkala, R. 2004: Bird species dynamics in a managed southern boreal forest in Finland. — *For. Ecol. Manage.* 195: 151–163.

Virkkala, R. & Liehu, H. 1990: Habitat selection by the Siberian tit *Parus cinctus* in virgin and managed forests in northern Finland. — *Ornis Fennica* 67: 1–12.

Väisänen, R. A., Järvinen, O. & Rauhola, P. 1986: How are extensive, human-caused habitat alterations expressed on the scale of local population in boreal forests? — *Ornis Scand.* 17: 282–292.

Wennström, U. 1991: *Kottförekomst och frökvalitet insamlingssäsongen 1991/92*. Information Skogsträdsförädling, Inst. f. skogsförbättring, Nr. 1, 1991/92.

Widén, P. 1987: Goshawk predation during winter, spring and summer in a boreal forest area of central Sweden. — *Holarctic Ecol.* 10: 104–109.