Does fragmentation by logging reduce grouse reproductive success in boreal forests?

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In 1999 and 2001, we compared the population characteristics of capercaillie *Tetrao urogallus*, black grouse *T. tetrix* and hazel grouse *Bonasa bonasia* inside the pristine forest reserve State Natural Reserve 'Pinezhskiy' in northwestern Russia and in the logged forests surrounding the reserve. We also compared the abundance of mammalian predators and birds of prey. The August density of capercaillie was lower in logged forests than in the reserve ($P = 0.05$), but black grouse tended to be more abundant in the logged area ($P = 0.08$). For hazel grouse, no difference in abundance was found between the reserve and the logged area. Reproductive success of all three grouse species was generally higher in the logged area than in the reserve. A winter track survey indicated low abundance (< 1 track/10 km/24 hours) and no difference in density of small and medium-sized mammalian predators between the reserve and the logged area. The only exception was red fox *Vulpes vulpes* whose tracks were recorded only in the logged area. Buzzards *Buteo* spp. and goshawk *Accipiter gentilis* were the most numerous birds of prey. Goshawk tended to be more common in the reserve ($P = 0.09$), whereas buzzards were seen more often in the logged area ($P = 0.1$). Tracks of mountain hare *Lepus timidus* was twice as abundant in the logged forest ($P = 0.02$), whereas tracks of red squirrel *Sciurus vulgaris* was almost 10 times more numerous in the reserve ($P < 0.001$) than in the logged area. Judged by the remains found, the majority (72%) of grouse were killed by birds of prey. Our study suggests that reproduction of all three species of forest grouse in this region remains stable or increases following logging. We hypothesise that this may be due to the type of logging performed and to differences in the composition of predators and of prey other than grouse inside and outside the reserve.

Key words: forest grouse, logging, northwestern Russia, predation

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A number of studies show predation to be the most important direct mortality factor in grouse, and both temporal and spatial variation in grouse reproductive output seem correlated with variation in predation pressure (Hagen 1952, Hørnfeldt 1978, Angelstam 1984, Kurki, Helle, Lindén & Nikula 1997). The possibility that predation pressure on grouse increases in forests subjected to clear-cutting and block treatment rather than to selective cutting of single trees, which used to be the typical logging method, has received considerable attention (Hansson 1994, Henttonen 1989). Increased predation in boreal forests may be a functional (i.e. it has become easier for predators to find broods; Storaas, Kastdalen & Wegge 1999), and/or a numerical response (Storaas & Wegge 1987, Kurki, Nikula, Helle & Lindén 1998, Kurki, Nikula, Helle & Linden 2000). To explain the latter, it has been suggested that clearcuts and young forest with open canopy favour forest-dwelling, generalist predators by increasing areas with grass-dominated field vegetation which make up optimal habitats for their preferred prey, *Microtus* voles (Hansson 1994, Henttonen 1989, Wegge, Rolstad & Gjerde 1992).

Despite much interest in the effect of modern forestry on the fauna, few studies have provided empirical data on grouse mortality in relation to degree of fragmentation within the forest landscape. A main difficulty in the study of this important aspect of grouse ecology is lack of stands of mature forest that are sufficiently large to be used as reference areas. As a local population of capercaillie *Tetrao urogallus* uses some 100 km^2 during the breeding cycle (Rolstad & Wegge 1987), and considering the impact of surrounding fragmented forests on the unlogged forest, mature forests to be used as reference areas should preferably be several 100 km^2. Whereas large undisturbed reference areas are no longer available in Fennoscandia, such old growth forests are still found in the Russian 'zapovednik' (nature reserve) system. In this paper, we compare populations of capercaillie, black grouse *T. tetrix* and hazel grouse *Bonasa bonasia* within a large reserve of old-growth forest in northwestern Russia, with that of the surrounding area of logged forest. We test the hypothesis that logging causes the reproductive performance of forest grouse to decrease and the density of generalist predators to increase.

Study area

The study area is located in the Archangelsk region in northwestern Russia on the southeastern part of the Belomoro-Kuloyskoe plateau (64° 42'N, 42° 67'E). The climate is continental with mean temperatures of 14.3° C in July (the warmest month) and -14.7° C in January (the coldest month). Snow covers the ground from late October to mid May. The area has a gentle topography with altitudes between 50 m and 150 m a.s.l. The fieldwork was carried out in the 421 km^2 Pinega Reserve and an adjacent 540 km^2 logged area. The forests belong to the northern sub-zone of coniferous forest with spruce *Picea obovata*, *P. obovata* x *P. abies* and Scots pine *Pinus silvestris* as the dominating tree species intermingled with scattered larch *Larix sibirica*. The reserve forms part of the Russian Zapovednik-system and is strictly protected for scientific purposes. Only scientists and rangers have legal access to the reserve.

Continuous spruce forests, that are more than 120 years old, dominate the reserve (Table 1) and have mainly been rejuvenated by forest fires, though only minor fires have occurred after 1960. Burned areas from before the 1960s are located in the eastern part of the reserve. The forests of secondary successions are dominated by birch *Betula pendula* and *B. pubescens*, with an understory of spruce and pine, and intermixed with patches of old spruce and pine that survived the fires. Large bogs are located in the southwestern part of the reserve, and smaller bogs are intermixed in the forest throughout the reserve.

Outside the reserve, extensive logging has been carried out during the last 50-60 years. Logging has progressed from stands of high value to those of lesser value. The densest, often pine dominated stands, have generally been cut first, leaving the rest of the forest in a highly fragmented condition. Forestry of the region operates on a larger scale than in most west European countries. The average size of clearcuts in our study area is close to 1 km^2, but some are as big as 20 km^2 (see Table 1). Patches of less valuable timber and single trees are generally left within the large clearcuts. Today, mature forests, in scattered stands, comprise about 40% of the area surrounding the reserve. Patch sizes may be up to more than 10 km^2, but the average size is 1-2 km^2 (see Table 1). In the logged area, there is a moderate to light hunting pressure on grouse.

The fauna is typical for northern boreal forests. There

Table 1. Area coverage (in %) and average patch size (in km^2) of the dominating forest types in the Pinega Forest Reserve and the surrounding logged area.

	% area coverage		Average patch size (km^2) in logged area		
Forest type	Reserve	Logged area	$\bar{x}$	± SE	Range
Mature pine forest (> 80 years)	1.7	14.7	0.51	± 0.15	0.01 - 5.10
Mature spruce forest (> 80 years)	50.6	15.9	1.79	± 0.46	0.04 -11.72
Mature mixed forest (> 80 years)	11.1	10.2	1.3	± 0.23	0.07 - 4.85
Bogs	10.1	3.3			
Secondary forest (20-60 years)	26.5	42.2	2.75	± 1.03	0.01 -35.40
Clearcuts and burns (< 20 years)	0	13.7	0.89	± 0.26	0.04 -19.19

is a population of cervids such as moose *Alces alces*, but the overall density is low, estimated at 2-3 animals/10 km^2 (Danilkin 1999).

Methods

Grouse (capercaillie, black grouse and hazel grouse) were counted along survey lines during 10-26 August 1999 and 1-28 August 2001, respectively. The survey lines traversed both the centre of the reserve and typically logged areas to the north of the reserve. The survey lines were spaced at 1 km intervals and followed pre-marked transects in a north-south direction. The counting was carried out by seven people, who worked individually and used a dog to detect the birds. The counters worked in two teams, one in the reserve and the other in the logged area, and they changed census areas midway in each survey period. All survey lines were walked once a week. When flushed, each bird was recorded according to species, sex, age and, if present, size of brood. Also, the perpendicular distance from the survey line to the site of flushing was estimated, and the location of each bird was plotted on a forest map. On the basis of forest maps, the reserve forests and the logged area were divided into six types: mature pine forest, mature spruce forest, mature mixed coniferous forest, bogs, secondary (young) forest and clear cuts/burned areas (see Table 1).

A density index for birds was estimated by dividing the number of birds flushed with the area surveyed. The area surveyed was computed by multiplying the length of survey lines with twice the average perpendicular flushing distance. Flushing distance was determined separately for species, sex, age and brood, and for the six types of habitats. If significant differences in flushing distances for either of these categories were found, these were used when density was computed. Mean flushing distance varied between 42.6 m (adult male capercaillie) and 7.8 m (hazel grouse). Capercaillie, black grouse and hazel grouse, which flushed beyond 100, 70 and 30 m, respectively, were not included in the density estimates. For the statistical analyses, the survey lines were divided into sections of 20 km, which were used as units of bird density. The 20-km sections were chosen as this was the distance at which the estimated density of capercaillie (i.e. the least common species) began to stabilise.

Abundance of mammalian predators, as well as the rodents red squirrel *Sciurus vulgaris* and mountain hare *Lepus timidus*, inside and outside of reserve, was estimated by counting tracks in the snow during the week 27 February - 2 March 2001. These track surveys were made along the sections of the survey lines used for grouse counts, and represented a typical habitat composition. A standard method, routinely used in Russian game management and nature reserves, was applied: each survey line was walked twice. Tracks were obliterated during the first survey, and new tracks crossing the survey lines were counted during the following day. The number of tracks counted is used as an index of relative abundance expressing crossings per 24 hours per 10 km of survey lines. The length of survey lines was 251.8 km inside and 283.8 km outside the reserve.

Birds of prey were recorded outside and inside the reserve: using the distance from a counter at which the bird was first detected to a bird, a density index was estimated by the same method as applied for grouse. Prey remains of grouse and hare were recorded during the grouse survey in August, and additionally for grouse remains were also collected along transects walked in the spring, early summers and winters of 1999, 2000 and 2001, giving a total transect length of 2,436.7 km inside and 2,903.6 km outside the reserve. When our data were normally distributed, we used the t-test to test for difference in abundance, and when not normally distributed, we used the non-parametric Wilcoxon signed-rank test (Siegel & Castellan 1989).

Table 2. Average density of capercaillie, black grouse and hazel grouse (birds/km^2) inside the Pinega forest reserve and in the logged area outside the reserve expressed as average of all forest types, in old spruce forest (> 80 years) and in young forest (10-60 years). The surveys were conducted in August of 1999 and 2001. Differences between density estimates were tested using the Wilcoxon signed-rank test.

		Inside reserve			Outside reserve			
Species	Habitat	X	N*	SE	X	N	SE	P
Capercaillie	All forest types	6.2	65	0.6	3.6	82	0.5	0.002
	Old spruce forest	6.4	32	0.8	5.7	17	1.1	0.146
	Young forest	5.7	15	1.5	2	10	0.9	0.022
Black grouse	All forest types	5.4	65	1	7	82	1	0.088
	Old spruce forest	3.9	32	0.8	4.2	17	1.1	0.455
	Young forest	3.6	15	0.9	11.3	10	2.2	0.003
Hazel grouse	All forest types	46	65	5.2	44.3	82	3.2	0.483
	Old spruce forest	55.8	32	3.3	57.8	17	5.6	0.45
	Young forest	64.4	15	5.9	58.3	10	6.8	0.38

* Number of 20-km transect sections

Table 3. Track crossings per 10 km of survey lines per 24 hours of carnivorous mammals, mountain hare and red squirrel. Recordings were made inside the Pinega forest reserve and in the logged area outside the reserve during February 2001. Differences between numbers of crossings were tested using Wilcoxon signed-rank test.

	Inside reserve			Outside reserve			
Species	Tracks/10 km	N*	SE	Tracks/10 km	N	SE	P
Stoat and weasel	4.62	10	1.91	3	20	0.85	0.208
Wolverine	0	20	-	0.03	24	0.03	-
Otter	0.04	20	0.04	0	24	-	-
Pine marten	0.7	20	0.27	0.64	24	0.39	0.24
Red fox	0	20	-	1.02	24	0.34	-
Lynx	0.11	20	0.08	0.28	24	0.12	0.262
Sum carnivores	0.77	20	0.25	1.88	24	0.65	0.198
Mountain hare	24.6	10	3.78	53.54	9	10.03	0.019
Red squirrel	42.86	10	7.05	4.34	9	0.73	<0.001

* Number of 10-km transect sections

Results

During August 1999 and 2001, a total of 3,343 grouse (697 capercaillie, 768 black grouse and 1,878 hazel grouse) were recorded along 2,653 km of survey lines. Most of our work (89% of survey lines) was carried out in 2001. Comparing the results obtained in the logged area to those from the reserve, the density of capercaillie was highest in the reserve, whereas black grouse tended to be more abundant in the logged area (Table 2). The density of hazel grouse did not differ between the reserve and the logged area (see Table 2). Comparable patches of old growth spruce forest in the reserve and in the logged area had similar densities of all three grouse species. The differences in overall densities of grouse between the reserve and logged area were mainly caused by fewer capercaillie and more black grouse in the young forest of the logged area (see Table 2). The density of hazel grouse, on the other hand, was similar in the young forest of the two areas. For herbivorous mammals, track surveys indicated 10 times higher density of squirrels in the reserve (43 tracks/10 km/24 hours) than in the logged area (4.3 tracks/10 km/24 hours), whereas tracks of mountain hare were twice as numerous in the logged area (53.5 tracks/10 km/24 hours) than in the reserve (24.6 tracks/10 km/24 hours; Table 3).

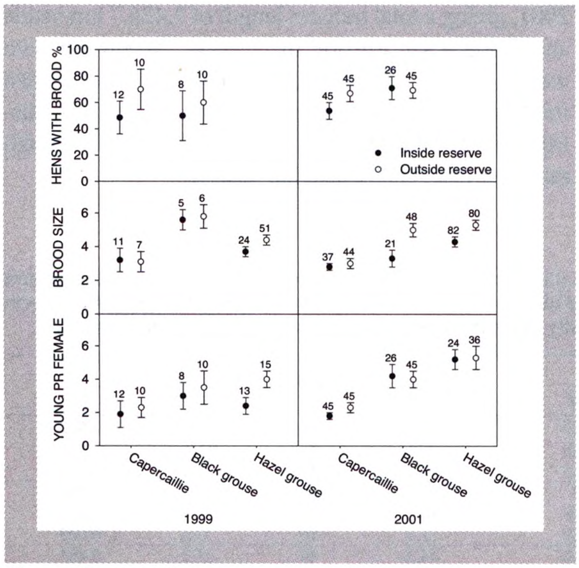

Figure 1. Reproductive success of capercaillie, black grouse and hazel grouse inside the Pinega forest reserve and in the logged area outside the reserve, during August 1999 and 2001. Bars show standard error.

The reproductive success (e.g. brood size, proportion of hens with chicks and the number of young per hen) were, generally, higher in the logged area for all three species of grouse (Fig. 1), and the difference was significant for proportion of hens with chicks for capercaillie in 2001 (Z = 1.68, P = 0.05), for brood size of hazel grouse in 1999 (Z = 1.66, P = 0.05) and 2001 (Z = 2.66, P = 0.004), for black grouse in 2001 (Z = 2.25, P = 0.012) and for chicks per hazel grouse hen in 1999 (Z = -2.56, P = 0.005). Higher, but not significantly higher, values for the logged area were also found for proportion of capercaillie and black grouse hens with chicks in 1999, for black grouse brood size in 1999, capercaillie brood size in 2001, chicks per capercaillie hen in 1999 and 2001, chicks per black grouse in 1999 and chicks per hazel grouse in 2001 (Z = -1.35-0.99, P = 0.09-0.47; see Fig. 1).

The track survey indicated no difference in abundance of small and medium-sized predators in the logged area compared to the reserve, except for red fox *Vulpes vulpes* whose tracks were recorded only in the logged area (see Table 3). Stoat *Mustela erminea* and weasel *M. nivalis* were the most abundant predators both in the reserve and the logged area. In the logged area, there was no difference in number of tracks/10 km between pine marten *Martes martes* and red fox. The larger predators wolverine *Gulo gulo*, lynx *Lynx lynx* and otter *Lutra lutra* were encountered infrequently in both areas (see Table 3).

Of predatory birds, 11 species were recorded. Among these, common buzzard *Buteo buteo*, rough-legged buzzard *B. lagopus* and goshawk *Accipiter gentilis* were the species most frequently observed. More goshawks were seen in the reserve (17.1/100 km^2) than in the logged area (10.2/100 km^2; Z = - 1.33, P = 0.092), whereas buzzards demonstrated an opposite trend, with more birds seen in the logged area (11.7/100 km^2) than in the reserve (6.9/100 km^2; Z = 1.23, P = 0.109).

Of 100 remains of dead grouse found during the survey work (1.7 remains/100 km), the cause of death was determined for 82 birds by visual inspection. The majority (72%) were killed by birds of prey and the rest (28%) by predatory mammals. The proportion of birds killed by the two groups of predators was almost identical in the reserve and the logged area (71% and 73%). Equal frequencies of remains were found in the logged area and in the reserve, with hazel grouse as the dominating species (46%), followed by capercaillie (38%) and black grouse 16 (%).

Hare remains were more abundant in the logged area (1.1/100 km) than in the reserve (0.1/100 km^2; Z = 2.29, P = 0.011).

Discussion

Our hypothesis, that reproductive success would be lower in the logged area than in the reserve, was refuted. Both the proportion of hens with chicks and brood sizes tended to be higher in the logged area for all three species of grouse than in the reserve. There may be at least three explanations for this: 1) the initial hypothesis is wrong; logging may not be beneficial to generalist predators and consequently predation pressure on eggs and chicks is not altered; 2) the particular logging methods applied in this area cause no negative effects, directly or indirectly, to grouse reproduction; and 3) due to the particular ecological conditions of this northern region, small and medium-sized predators respond differently to the logging itself than predators at more southern latitudes.

Modern forestry and generalist predators

The generalist predators assumed to benefit from forest fragmentation and increasing areas of young forest are red fox, the smaller species of *Mustelidae*, stoat and weasel and, to a lesser extent, the pine marten. Track surveys during winter in Scandinavia have demonstrated a positive relationship between areas of young forest and track density of red fox (Kurki et al. 1998, Gundersen & Rolstad 2000). In southeastern Norway, capercaillie broods (during summer) and subadult males (during winter) were predated at a lower rate within blocks of unfragmented, old forest than in surrounding fragmented forests (Wegge, Gjerde, Kastdalen, Rolstad & Storaas 1990, Gjerde & Wegge 1989). Furthermore, nest predation appears to be extremely high in fragmented forests (Storaas, Wegge & Larsen 1985). However, the relationship is complicated by an apparent habitat/food related component; there was no relationship between fox density and the proportion of hens with broods in southern Finland (Kurki et al. 1997), but in northern Finland, an increase in red fox density was negatively correlated with the probability of an observed grouse hen being with a brood in low vole years, whereas in years of high vole density no correlation was detected (Kurki et al. 1997). For pine marten, density of tracks shows little relationship to young forest. Although older forest is preferred, this species is capable of using a wide variety of forest types (Grakov 1981, Brainerd 1997, Kurki et al. 1998, Gundersen & Rolstad 2000). Of the other generalist predators, the stoat appears to be of minor importance as a nest and brood predator in forest grouse compared to red fox and pine marten (Kurki et al. 1997).

Although the few studies that have been carried out indicate a positive effect of forest fragmentation on abundance of generalist predators, it may be argued that because forests on better soils have been cut first and those on poorer soil quality remain (NIJOS 2000), the higher density of predators in fragmented forests is related to more food on better sites, rather than to fragmentation *per se*. In the Pinega district, there may be an opposite effect. Generally, the most productive forest types (mostly spruce) are found on patches with very rugged karst relief (craters interspersed with abrupt ridges and canyons) or in river valleys (Saburov 1972, Puchina 2000). Logging within karst areas is difficult, and in river valleys logging is prohibited in Russia (Melekhov 1989). As a result of this, the majority of clearcuts in the district are found on sites of lower productivity such as in dry, upland pine forests and in boggy, flat areas.

Whereas a numerical response by predators to forest fragmentation may explain high egg losses (Storaas & Wegge 1987), a functional response has been suggested to explain higher chick losses (Storaas et al. 1999). Because chicks' choice of feeding sites are predictable, predators may develop a search pattern for the limited areas of the habitats remaining in the fragmented patches of old forest (Wegge et al. 1990). Empirical data on predator habitat use to evaluate this hypothesis are highly needed.

Contrary to the situation in Europe (see Storch 2000 for a review), forest grouse have maintained most of their historic range in North America, and their populations are stable (Boag & Schroeder 1992, Zwickel 1992). Predation loss, however, may be substantial and appear to be comparable to that of grouse in Europe (Hewitt, Keppie & Stauffer 2001). Concealed nests of forest grouse suffer lower loss due to predation (Boag, Reebs & Schroeder 1984), but there has been no studies in North America indicating higher predation risk due to forestry. Red fox has increased in numbers in much of the cultivated parts of the Prairie Region of North America (Johnson, Sargeant & Greenwood 1989), but no increased abundance of small and medium-sized predators has been reported from forested regions subjected to modern logging methods (Hewitt et al. 2001).

To conclude, predation loss in forest grouse as well as the density of red fox appear to have increased in Scandinavia during recent decades (Christiansen 1979, Hjeljord 1980, Lindström 1987, Kurki et al. 1998). Although there is some evidence that this may be due to modern forestry with increasing fragmentation and areas of young forest, a rigorous test of this hypothesis has yet to be done.

Forest grouse and logging methods

Logging outside the reserve has caused a coarse-grained forest mosaic (see Table 1), but single trees as well as groups and patches of trees of little economical value are left within clearcuts and stands of young forest. In spite of the large logging units, this gives the area a heterogeneous composition. The effect of logging on the density of vertebrate herbivores was as expected; an increase in the early successional species (hare and black grouse) and a decrease in old forest species (capercaillie and red squirrel). In the remaining patches of old spruce forest in the logged area, the density of all three grouse species was similar to the density in the larger stretches of old spruce forest within the reserve, indicating no overall edge effect from predators. In the young forest of the logged area, the density of capercaillie was lower compared to the young (mostly fire-induced) forest of the reserve. Interestingly, the density of hazel grouse was similar in the young forest of the reserve and in the young forest outside the reserve. Also in other regions influenced by modern forestry, like in Finland and in the upper drainage of the Pechora River to the east of our study area, hazel grouse has either decreased less than the other grouse species, or their numbers have remained stable (Lindén & Rajala 1981, Beshkarev, Blagovidov, Sokolski & Hjeljord 1995). From Komi, southeast of the Archangelsk region, Romanov (1963) reported almost similar densities of hazel grouse in logged and un-logged areas, whereas capercaillie showed an almost three-fold decrease in abundance in logged forest (Romanov 1979). Russian grouse scientists believe that the hazel grouse survive well in dense natural regrowth following logging (Romanov 1963, Jurgenson 1968, Andreev 1981).

We lack data to judge whether the logging methods applied in the study area are especially 'grouse friendly', but the small and large patches of remaining old forest may be of importance in this connection.

Predation in the taiga of the Russian North

Tracks of pine marten and stoat/weasel did not differ inside and outside the reseve. Similarly, there was no difference in track abundance of these predators in logged areas compared to pristine forest around the upper Pechora River to the east of our study area (Beshkarev et al. 1995). Track surveys in Finland showed the red fox in the north to be the only predator that increased in numbers with forest fragmentation (Kurki et al. 1998). Also in our study, tracks of red fox were recorded only in the logged area outside the reserve. In the forests of northern Russia, with loose and deep snow, the red fox is rare and is mostly found around villages and on agricultural land (Vaisfeld 1985). Within the reserve, the red fox has not been recorded during the last 10 years of track surveys (Rykov 2000). We encountered only one fox track/10 km/24 hours compared to 4.4 and 12.3 tracks/10 km/24 hours reported from the wildlife triangle surveys in northern and southern Finland (Kurki et al. 1998), respectively. Contributing to the low number of foxes in our area may be a lack of cyclicity and a decrease in the microtine rodent population over the last 10 years (Kuprianova & Sivkov 2000). More pine marten tracks were recorded in our study (0.6-0.7 tracks/10 km/24 hours) than in northern Finland (0.3 tracks/10 km/24 hours), but less than in southern Finland (1.4 tracks/10 km/24 hours).

The generally better reproduction of grouse outside the reserve indicates that there are no numerical or functional effects from generalist predators on grouse following forest fragmentation and increased areas of young forest. On the contrary, our data indicate higher losses to predation within the old forest of the reserve. The main grouse predator in the old forest is probably the goshawk (Sulkava 1964, Tornberg 1997). This raptor is associated with old forest (Widén 1985) and was also observed by us more frequently inside the reserve. Furthermore, grouse remains showed avian predators to be the most important cause of mortality both inside and outside the reserve. Another factor contributing to higher reproductive success of grouse in the logged area may be the higher population of hares which act as a buffer and reduce the predation on grouse eggs and chicks compared to the old forest of the reserve. This, rather than predation by goshawk, could explain the higher percentage of hens without broods (indicating complete loss of clutches) in the reserve than in the logged area.

To summarise, our study suggests that the effect of forest fragmentation on grouse abundance and reproduction may be more dynamic and spatially and temporally more variable than has previously been assumed. It should be remembered that conditions vary over the vast expanses of the northern, boreal forest. Our knowledge of this important aspect of forest and grouse management is still limited.

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