

Comparing predation on forest grouse nests by avian and mammalian predators in two contrasting boreal forest landscapes by the use of artificial nests

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Egg predation is an important determinant of breeding success among boreal forest grouse, but the relative roles of mammalian and avian predators are poorly known. During spring/early summer of 2010, predation on artificial nests was studied by placing nests on the ground and on 1.5-m tall poles at two forested areas. One study site was highly fragmented due to intensive forestry (Varaldskogen, Norway) and the other site was a pristine, natural forest in north-western Russia (Pinega Forest Reserve). The nests on poles were subject to predation by birds and those on the ground by both mammals and birds. Total predation was significantly higher in Varaldskogen than in Pinega. Ground nests suffered ca. 2.5 times higher losses than nests on poles. In Pinega, predation did not differ between the two nest types. The difference between the two areas was probably due to different predator guilds: mammalian generalist predators, such as the Red Fox (*Vulpes vulpes*) and Badger (*Meles meles*), were common in Varaldskogen but scarce or absent in Pinega. Canopy cover explained most of the variation in predation rate in Varaldskogen, but no significant relationship with canopy or nest concealment was detected in Pinega. Predation on pole nests varied across habitat types in a similar manner at the two areas, but predation on ground nests did not. As Raven (*Corvus corax*) and Hooded Crow (*Corvus corone cornix*) were rare in both areas, these findings suggest similar searching and predatory behaviour of the two main (smaller) corvids, the Eurasian Jay (*Garrulus glandarius*) in Varaldskogen and the Siberian Jay (*Perisoreus infaustus*) in Pinega. Although the study design allowed a comparison between avian and mammalian nest predators, the lack of a clearer relationship between predation and certain variables suggests that nest predation is a complex process involving components of predator behaviour.



1. Introduction

Boreal forest grouse have high innate reproductive capacity; females of all species breed as yearlings, and clutches vary between 7 and 12 eggs (Johnsgaard 1983). Besides chick loss, predation of eggs is a major factor determining annual breeding success, i.e., the number of chicks recruited into the autumn population (Wegge & Storaas 1990, Moss & Watson 2001). Both mammals and birds prey on grouse nests, but the relative roles of these two groups are poorly known, mainly because signs from depredated nests cannot readily be assigned to species or species group (Larivière 1999). Obtaining accurate information on who robs nests requires monitoring by the use of remotely-triggered photographic equipment, usually in combination with radio telemetry. Such technology is expensive and therefore limits the number of nests that can be monitored, in turn limiting the inference that can be made for the study population as a whole.

Artificial nests have been widely used to estimate egg predation of ground-nesting birds, including grouse (Loman & Göransson 1978, Andrén *et al.* 1985, Angelstam 1986, Storaas 1988, Andrén 1992, Huhta *et al.* 1996, Svoboda *et al.* 2004, Storch *et al.* 2005, Klausen *et al.* 2010, Støen *et al.* 2010). However, because eggs in artificial nests are not incubated by a cryptically-coloured female, such nests are more exposed than natural nests. Also, by lacking olfactory cues, the detection efficiency of scent-oriented mammalian predators, such as the Red Fox *Vulpes vulpes*, is reduced.

A combination of these factors leads to biased information about the rate of loss and the relative role of predators hunting mainly by sight or by scent (Storaas 1988, Willebrand & Marcström 1988, Zanette 2002, Burke *et al.* 2004, Thompson & Burhans 2004), the former presumably consisting mainly of avian predators. Acknowledging this limitation, artificial nests have still been considered a useful tool for uncovering the relative abundance and composition of these two groups of nest predators (Huhta *et al.* 1996, Major & Kendal 1996, Storch *et al.* 2005). Camera and video monitoring of nesting of the Greater Sage Grouse *Centrocercus urophasianus*, however, has demonstrated that it is virtually impossible to separate the

two predator groups on the basis of egg shells and nest remains (Coates *et al.* 2008).

Our objective was to compare the composition and abundance of grouse nest predators in two contrasting forest landscapes: Varaldskogen in Norway, consisting of a mosaic of different-aged forests originating from intensive forestry; and Pinega Forest Reserve in Russia, consisting of pristine, near-natural forest. Egg predation is presumably higher in Varaldskogen than in Pinega, owing to a higher abundance of generalist predators facilitated by clear-cutting forestry in the former (Angelstam 1986, Wilcove *et al.* 1986, Small *et al.* 1988, Andrén 1992) and close proximity to adjacent farmlands (Andrén *et al.* 1985, Huhta *et al.* 1996, Kurki *et al.* 2000, Storch *et al.* 2005). We placed artificial nests both on the ground and on poles. By placing nests on poles – instead of making artificial nest cups on tree stems (Yahner & Scott 1988, Nour *et al.* 1993) – we effectively eliminated arboreal mammals, thereby enabling us to make an inference on the relative importance of the two groups of predators in the two forest landscapes.

2. Material and methods

2.1. The study areas

Varaldskogen covers ca. 40 km² and is situated at 60°10'N, 12°30'E in south-eastern Norway. The forested area is bordered by scattered human settlement in the north and south where also farming takes place. The forest has been intensively managed for hundreds of years. During the past 50–60 years, the predominant logging method has been clear-cutting of 4–20-ha blocks, which have in turn been regenerated through planting or retaining scattered seed trees, leading to even-aged stands of either Norway spruce *Picea abies* or Scots pine *Pinus sylvestris*. These conifers are often interspersed by birch *Betula* spp. and aspen *Populus tremula*. In mature spruce-dominated forest, bilberry *Vaccinium myrtillus* dominates the field layer, which is largely replaced by graminoids after logging. In pine-dominated forests, heather *Calluna vulgaris* and cowberry *Vaccinium vitis-idaea* dominate the field layer. For further information concerning the area, see Wegge &

Table 1. Indices of abundance of main mammalian nest predators in Varaldskogen, Norway and Pinega Forest Reserve, Russia, derived from snow-tracking and expressed as mean \pm SE no. tracks/10 km * 24 hours^a. Significant differences ($p < 0.05$) are in bold letters.

Species	Varaldskogen ^b	Pinega ^c
Pine Marten	1.0 \pm 0.31	1.8 \pm 1.02
Red Fox	3.1 \pm 0.94	0.06 \pm 0.01
Stoat/Weasel	1.3 \pm 0.68	3.8 \pm 1.61
Red Squirrel	2.8 \pm 1.13	7.1 \pm 2.11

a) Badger was not sampled (see text).

b) J. Rolstad and P. Wegge, unpubl. data (2006–2010).

c) Adapted from Borchtchevski *et al.* (2003) and A. V. Sivkov, unpubl. data (2004–2010).

Rolstad (2011). – Spring density of the Capercaillie *Tetrao urogallus* and the Black Grouse *Tetrao tetrix* is approximately 2.5 and 3.3 individuals/km², respectively (P. Wegge, unpubl. data). Nest predation on natural and artificial nests has been intensively studied at the Varaldskogen area in the 1980s (Storaas & Wegge 1987, Storaas 1988, Wegge & Storaas 1990).

The 515-km² Pinega Forest Reserve is located at the upper drainage of the Pinega River, ca. 300 km south-east of Archangelsk, in north-western Russia (64°35' N, 43°02' E). The reserve was established in 1974 and is a part of the Russian zapovednik system, a nature-conservation area network. As a protected area with strict regulations of human activity, it is dominated by pristine, mixed coniferous forest interspersed with scattered, small patches that have been either naturally burned or logged before the reserve was established. Siberian spruce *Picea obovata* and the hybrid spruce *P. obovata* \times *P. abies* are the dominant tree species, covering about 75% of the landscape, either in pure stands or inter-mixed with Scots pine and Siberian larch *Larix sibirica*. Open peat bogs and lakes make up about 11% of the landscape. The large expanses of old forest are typically two-layered, with trees older than 120 years dominating the overstory and trees of 40–60 years of age the understory. The field layer consists mainly of a mixture of ericaceous shrubs, but owing to limestone-rich soils, forbs often dominate in moist depressions. For further information, see Wegge *et al.* (2005) and Rolstad *et al.* (2009). – At the time of the study, densities of the Capercaillie and the

Black Grouse were slightly higher and lower, respectively, than in Varaldskogen, and Hazel Grouse *Tetrastes bonasia* was particularly abundant in Pinega (Borchtchevski *et al.* 2003).

Mammalian predators had been sampled during winter at both study areas (Table 1). Red Fox was an abundant predator in Varaldskogen, but was nearly absent in Pinega. Similarly, Badger *Meles meles* was common in Varaldskogen, but did not occur in Pinega. We only have qualitative information on the relative abundance and composition of avian nest predators in the two areas. Hooded Crow *Corvus corone cornix* and Raven *C. corax* were scarce in Varaldskogen; during 12 days of field work, Raven was observed twice and no Hooded Crows. Eurasian jay *Garrulus glandarius* does not expose itself as readily as the above-listed, larger corvids; as a rough indication of abundance, this bird was usually encountered 1–2 times each week during summer and more frequently during winter (P. Wegge, unpubl. data). The Pinega Forest Reserve is >50 km from the nearest village, and had no crows and only occasional Ravens (seen twice in 7 weeks). The Siberian Jay *Perisoreus infaustus* appeared the main corvid there, observed nearly daily during the 7 weeks of field work. The two species of jay thus apparently were the main avian egg predators at the two areas, supplemented by Ravens.

2.2. Field methods

2.2.1. Nest types

We used two types of artificial nests. In addition to conventional ground nests, we placed nests on poles: on top of a 1.5-m tall, cut and pruned sapling we attached a 30 cm \times 30 cm plywood board and covered it with a few cm of moss. To reveal if ground predators had climbed and robbed the eggs, we covered a section of the pole with tape. Also, to prevent arboreal mammals (Red Squirrel *Sciurus vulgaris* and Pine Marten *Martes martes*) from jumping onto the nest, we placed poles well away from branches of larger trees and removed smaller trees within a 2–3-m radius of the poles, when necessary. Pole nests were presumably available to avian predators only, whereas ground nests were available to both avian and mammalian predators.

In both types of nests we put two brown chicken eggs, resembling Capercaillie eggs in size and colour. Nests were laid out along logging roads (Varaldskogen) and ca. 3-m wide cut transects (Pinega) as follows: from random starting points, ground and pole nests were placed alternatively on the left- and right-hand side of the road/transect, ca. 200 m apart, and the distance between similar nest types was 400 m. The perpendicular distance from the road/transect was 40–60 m, with location of the nest selected randomly. Because nesting sites of boreal forest grouse are variable (Storaas & Wegge 1987), the exact spot of the chosen ground nest mimicked that of natural nests. When setting the nests and checking them later, we wore plastic bags on rubber boots to avoid predators following our scent trail (Whelan *et al.* 1994, Hughes *et al.* 2010).

2.2.2. Nest-site measurements

Nest-site measurements were consistent between the two study areas. Habitat type was grouped into four classes: open area, young forest, mature forest, and forest/open-area edge. In Varaldskogen, open areas were either up to 5-yr old clear-cuts, treeless bogs, or open, forested bogs with widely-spaced trees older than 70 years. Young forest was either planted (spruce) or was of seed-tree origin (pine) after logging, between 6 and 50 years old. Mature forest was, if artificially regenerated, 50–70 years or, if naturally regenerated, 70 years old pine or spruce forest. Edge was the transition zone between forest and bog or clear-cut within 10 m from the edge.

In Pinega, open areas were either treeless or forested bogs. Young forest was 2–6 m tall, naturally regenerated after a wildfire, dominated by birch inter-mixed with pine and spruce and up to 30-m tall, solitary larch trees. Mature forest was dominated by spruce inter-mixed with larch, pine and birch, typically in two or three layers.

For ground nests, we measured nest concealment from above (NCA) and vertically within 5 m (NCV), following Storaas (1988). When estimating NCA, we placed a 30 cm × 30 cm plywood board, with 100, 3 cm × 3 cm black and white squares, horizontally onto the nest and counted – with one eye closed – the number of visible

Table 2. Numbers of artificial nests set in different habitat types in Varaldskogen and Pinega Forest Reserve.

Habitat	Varaldskogen		Pinega	
	Ground	Pole	Ground	Pole
Open area	8	6	12	12
Young forest	32	12	17	11
Mature forest	25	12	41	48
Edge	31	17	5	4
Total	96	47	75	75

squares seen from above. When estimating NCV, we placed the checkerboard vertically onto the nest and counted the number of visible squares from all four cardinal directions standing 5 m from the nest. The sum of NCA and NCV is hereafter referred to as ground cover.

Canopy cover was estimated by sitting down over the ground nest or as close as possible to the pole nest, leaning back and looking straight up, with one eye closed, and estimating the percent of visible sky (over canopy cover). For pole nests, only canopy cover was measured.

2.2.3. Nest distribution and visits

In Pinega, 75 pole nests and 75 ground nests were assigned along 5 transects between May 31 and June 8. In Varaldskogen, 48 ground nests and 47 pole nests were set on May 16, placed in the same manner as in Pinega, but along forest roads ($N=7$). After 12 days, a second batch of 48 ground nests was set >100 m from those nests that had already been predated. The distribution of nests across habitat types at each study area is shown in Table 2.

In Pinega, nests were checked for signs of predation three times at intervals of approximately 10 days. The eggs were out in the forest for 29–31 days, 3–5 days more than the incubation period of Capercaillie (Wegge & Storaas 1990). In Varaldskogen, nests were checked four times and were out for 24–27 days. Nests were considered depredated if at least one egg was missing or destroyed. When checking the nests, plastic bags were used on rubber boots in the same manner as when placing the nests.

2.2.4. Statistical analyses

We compared the proportions of nests depredated during 26 days. Prior to analysis, the number of depredated nests was adjusted to the period of 26 days by estimating daily survival (Mayfield 1975) during the last observation period in each area and then reducing (in Pinega) or adding (in Varaldskogen) the number of depredated nests accordingly; these resulted in only minor changes due to the small differences in exposure times. As an exploratory step, we first used binomial logistic regression to identify the relative importance of nest-cover and habitat variables (see section 2.2.2.). Because we knew the starting dates and exposure times, we did not apply the modified model developed by Shaffer (2004). We followed Lewis *et al.* (2004) when converting continuous variables to categorical data. Two-way contingency tests disclosed significant differences in predation rates on both ground and pole nests among transects in Pinega ($\chi^2 = 20.91$ and 20.85 , respectively; $df = 4$, $p < 0.01$ for both cases). Because these transects also varied in length and habitat-type composition, we considered transects a random variable and used generalized linear mixed-effects models for the data from Pinega. In Varaldskogen, nest predation did not vary significantly between transects, and the data were therefore analyzed using generalized linear models without mixed effects.

Model selection was based on the Akaike Information Criterion corrected for small samples (AICc) and the AICc (AICc for the model of interest minus the smallest AICc of all models considered). We also calculated the Akaike weights (wAIC) to judge the performance among models (Burnham & Anderson 2002). All models with $\Delta AICc$ value ≤ 2 were considered to have substantial support. Among these, further model selection was based on individual AICc values, Akaike weights and number of model terms.

After identifying the main factors by the linear models, we tested variation in predation between habitat types and nest types within each study area using two-way contingency tables or Fisher's Exact test in R. Similarly, we tested variation in nest-cover measurements for depredated and surviving nests using Wilcoxon or Kruskal-Wallis two-sample tests, and post-hoc comparisons with Dunn method for joint ranking, in JMP 9 (SAS Institute

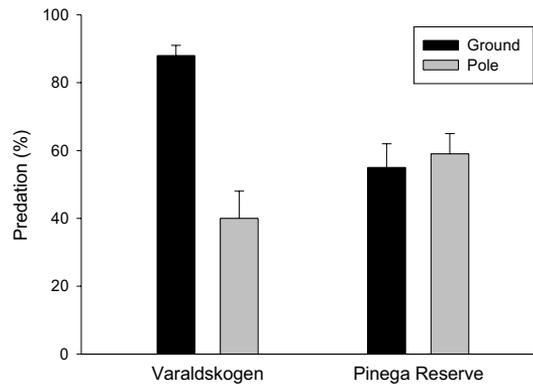


Fig. 1. Mean proportion (\pm SE) of artificial nests depredated during 26 days in Varaldskogen and Pinega in spring of 2010.

Inc. 2010). Owing to high predation on ground nests in Varaldskogen during the first few weeks, we compared losses of ground nests in different habitat types after 10 days of exposure time. For the other comparisons, exposure time was 26 days.

3. Results

Signs of nest predation were similar between nest types and the two areas; in most cases both eggs had been removed. In less than 10 percent of the depredated nests, egg shell pieces were observed within 10 m of the nest, and rarely inside the nest. We found claw marks on only one depredated pole nest, presumably made by a Pine Marten.

3.1. Predation and nest type

Total predation was significantly higher in Varaldskogen than in Pinega ($\chi^2 = 6.24$, $df = 1$, $p = 0.013$). In Varaldskogen, ground nests were depredated >2 times more frequently than pole nests ($\chi^2 = 32.69$, $df = 1$, $p = 0.001$; Fig. 1). In Pinega, predation did not differ significantly between nest types ($\chi^2 = 0.11$, $df = 1$, $p = 0.751$). The higher predation rate in Varaldskogen than in Pinega resulted from a significantly higher predation of ground nests in the former ($\chi^2 = 19.86$, $df = 1$, $p < 0.001$). The tendency for higher predation of pole nests in Pinega was not significant ($\chi^2 = 2.68$, $df = 1$, $p = 0.109$; Fig. 1).

Table 3. Generalized linear mixed-effects models of predation of ground nests and pole nests in Varaldskogen and in Pinega Forest Reserve, based on Akaike information criterion corrected for small samples (AICc). VS = Varaldskogen, PR = Pinega Reserve, N = number of observations, CC = canopy cover, NCA = nest concealment from above, NCV = nest concealment vertically, GC = ground cover, YF = young forest, MF = mature forest, EF = edge forest. Three best models for each category are shown; terms denoted with an asterisk contributed significantly ($p < 0.05$) to the selected model.

Response	N	Model	Terms	AICc	AICc	wAICc
<i>Varaldskogen</i>						
VS ground	96	1	CC*	114.14	0.00	0.386
VS ground	96	2	CC*+NCA	114.74	0.60	0.286
VS ground	96	3	CC*+GC	115.73	1.59	0.174
VS pole	47	1	CC	69.02	0.00	0.578
VS pole	47	2	YF+MF+FE	70.18	1.16	0.324
VS pole	47	3	CC+YF+MF+FE	72.56	3.54	0.098
<i>Pinega Forest Reserve</i>						
PR ground	75	1	YF+MF*+FE+GC	95.18	0.00	0.235
PR ground	75	2	YF+MF*+EF	95.34	0.16	0.216
PR ground	75	3	YF+MF+EF+NCV	95.59	0.41	0.191
PR pole	75	1	YF*+MF+EF	90.60	0.00	0.646
PR pole	75	2	CC+YF+MF+EF	92.37	1.77	0.266
PR pole	75	3	CC	94.59	3.99	0.088

3.2. The influence of habitat type and nest concealment on predation

Among the 19 models for the Varaldskogen data, AICc was ≤ 2 for three ground- and two pole-nest models. Canopy cover had the highest explanatory power for both nest types. For ground nests, nest concealment from above (NCA) was included in the second-best model, whereas for pole nests the second-best model included the habitat types young forest, mature forest, and edge. The three best models for each nest type are shown in Table 3.

Among the 18 models for the Pinega data, AICc was ≤ 2 for three ground- and two pole-nest models. The combination of three types of forest habitat was clearly the best model for both nest types, with ground cover (combination of vertical and horizontal cover at the nest site) also included in the best ground-nest model. In the second-best pole-nest model, canopy cover and the three habitat types were included. The three best models of each nest type are shown in Table 3.

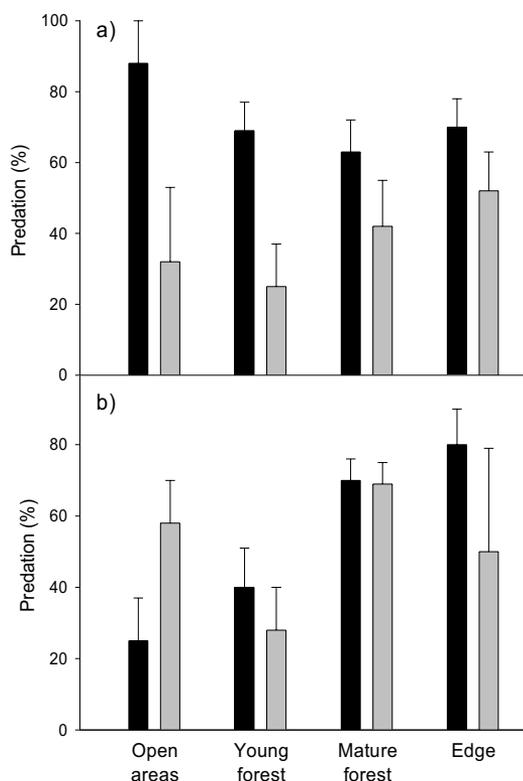


Fig. 2. Mean predation (\pm SE) of ground (black) and pole (grey) nests in different habitat types in (a) Varaldskogen and (b) Pinega.

Table 4. Canopy cover (%) of depredated (D) and surviving (S) artificial nests in Varaldskogen (VAR) and Pinega Forest Reserve (PIN) during spring 2010. Significant differences ($p < 0.05$) are in bold letters.

Habitat	VAR, Ground		VAR, Pole		PIN, Ground		PIN, Pole	
	D	S	D	S	D	S	D	S
Open habitat	9	10	0	2	16	9	2	3
Young forest	52	67	40	27	30	66	42	38
Mature forest	53	74	44	28	50	43	20	18
Edge habitat	52	54	26	33	37	8	12	21

3.3. Effects of habitat type and canopy cover on nest predation

The generalized linear models indicated that nest predation varied mainly with habitat type and canopy cover, and that most measurements of nest concealment were less important. Therefore, we examined these relationships more closely for each nest type at each study area.

In Varaldskogen, Fisher's exact test revealed no significant difference in either ground- or pole-nest predation between habitat types ($n = 96$ and 47 , $p = 0.204$ and 0.384 , respectively) (Fig. 2a). In Pinega, however, habitat type significantly influenced predation of ground nests ($n = 75$, $p = 0.018$; Fig. 2b). The ratio of ground/pole-nest predation was marginally higher in Varaldskogen than in Pinega in all habitat types ($t = 2.08$, $df = 6$, $p = 0.083$) except edge (Fig. 2).

Ground cover differed little between depredated and surviving nests in Varaldskogen, except for open sites where depredated nests were less concealed ($Z = 1.98$, $p = 0.047$). In Pinega, ground cover differed more between habitat types, being highest in young and mature forest. Here depredated nests were less concealed than those surviving, the difference being significant in mature forest ($Z = 2.07$, $p = 0.038$).

At Varaldskogen, canopy cover was lower for depredated compared to surviving ground nests among the four habitat types, but significantly so only in mature forest ($Z = 2.37$, $p = 0.018$; Table 4). For pole nests, canopy cover was slightly (non-significantly) higher among the predated nests in young and mature forests. In Pinega, the relationships were less clear; in three of the four habitat types, canopy cover was higher – not lower – on predated ground nests. Canopy cover was lower only in young forest for depredated ground nests

($Z = 2.10$, $p = 0.035$; Table 4). For pole nests, the pattern was similar to Varaldskogen.

The relationship between predation, canopy cover and habitat type is illustrated in Fig. 3. The condensed figure reveals one clear pattern: across all four habitat types, predation of ground nests in Varaldskogen decreased with increasing canopy cover ($b = -0.427$, $t = 12.0$, $p = 0.007$). There were no such relationships for ground or pole nests in Pinega or for pole nests in Varaldskogen. Moreover, habitat-specific predation rates related to canopy cover differed between the two study areas.

4. Discussion

Predation on artificial nests was higher in the more fragmented forested landscape in Varaldskogen than in the pristine forests of Pinega. This difference was due to a considerably higher predation of ground nests in the former, which was apparently caused by several factors. The human-impacted Varaldskogen had a high density of mammalian generalist nest predators, Red Fox and Badger, while these species were virtually absent in Pinega. The higher ratio of ground/pole-nest predation across three of the four habitat types supports this interpretation. Also, in an earlier study of real grouse nests in Varaldskogen, using radio telemetry, Storaas and Wegge (1987) inferred that mammals were far more important predators than corvid birds.

Eurasian Red Squirrel was more abundant in Pinega than in Varaldskogen, probably due to a larger relative cover of mature coniferous forest. As ground-nest predation in Pinega was rather small, nest predation by this species might be limited. This is surprising, as a previous study re-

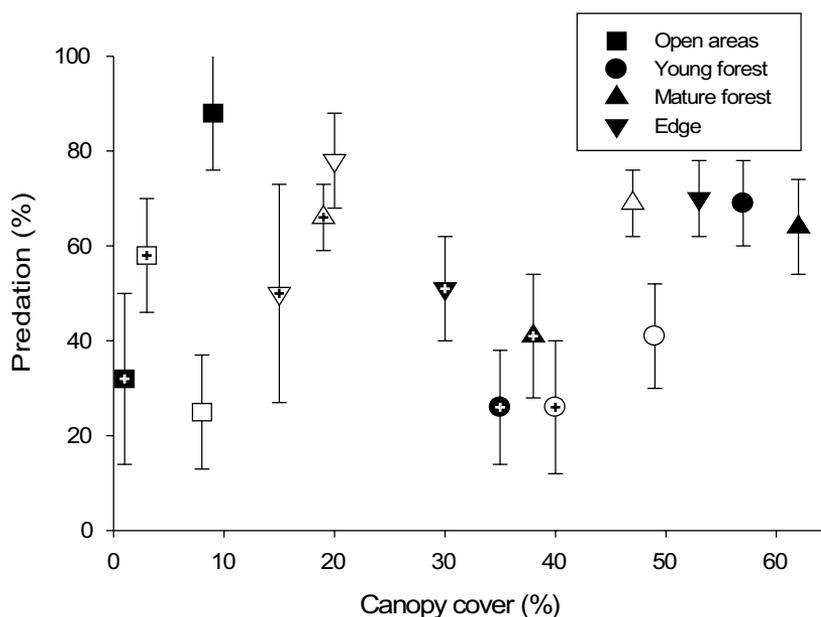


Fig. 3. Mean predation rates (\pm SE) at sites with different canopy cover. Ground nests are shown with filled black (Varaldskogen) or unfilled (Pinega) symbols. Pole nests are marked with + inside symbols.

ported high predation by the American Red Squirrel *Tamiasciurus hudsonicus* – a species quite similar to its Eurasian counterpart – on nests of the Spruce Grouse *Dendragapus canadensis* (Boag *et al.* 1984). However, because the eggs of this species are much smaller than those of the Fennoscandian forest grouse, the apparent small predation exerted by the Eurasian Squirrel might be explained by the relatively large-sized chicken eggs used in our study.

Most studies have concluded that generalist predators, such as corvids and Red Fox, are more abundant in fragmented than in contiguous landscapes, especially in close proximity to farmlands (Angelstam 1986, Andrén 1992, Rodewald & Yahner 2002, Svoboda *et al.* 2004). According to Hanski *et al.* (1991), the abundance of generalist predators also increases when moving southwards in the boreal region, probably due to higher general productivity and different prey communities between north and south (Andrén *et al.* 1985, Kurki *et al.* 1997). We therefore predicted higher avian predation of pole nests in Varaldskogen. Contrary to this expectation, corvids as a group appeared to be equally abundant in Pinega and Varaldskogen. Although located relatively close to human settlement, Ravens and Hooded Crows were rarely seen in Varaldskogen during summer and were less abundant than the Eurasian Jay. Si-

berian Jay was common in Pinega. It is smaller and has a smaller beak than its western counterpart, and its role as a predator of large grouse eggs is largely unknown. Nevertheless, because other corvids are rare in the reserve – but pole nests had still been frequently robbed – we believe that the Siberian Jay was the main avian predator in Pinega.

In Varaldskogen, ground nests were depredated about 2.5 times more frequently than nests on poles. Avian predators locate nests by sight, whereas mammals use both scent and visual cues. Ground nests were apparently preyed upon by both predator groups. Assuming corvids preyed on pole and ground nests at equal rates, the remaining proportion of robbed ground nests – in this case about half of the total loss of these nests – would be due to mammals. As jays were the main avian nest predators, this ratio of avian-to-mammalian predators on ground nests might have been true, as the jays – unlike the Hooded Crow and Raven – typically moves below the canopy layer and within the trees when searching for food. However, we cannot exclude the possibility that avian predation on pole nests was lowered due to their “unnaturalness”. We consider this unlikely, as the use of “strange” objects such as grease boards to identify egg predators did not deter corvids (Angelstam 1986, Huhta *et al.* 1996).

As the foraging behaviour of the Siberian Jay is relatively similar to that of the Eurasian Jay – both usually move below the canopy layer – and pole and ground nests were predated at equal rates in Pinega, the Siberian Jay could not have predated ground nests at the same rate as it predated pole nests: otherwise predation there by mammals would have been nil. The explanation is probably that, contrary to the Eurasian Jay, Siberian Jay avoids open areas, presumably in fear of the Goshawk *Accipiter gentilis* (Griesser & Nystrand 2009). This is supported, to some extent, by the observed habitat-specific predation rates: in Pinega, losses in ground nests in open sites were the lowest (26%) among all habitat types, whereas in Varaldskogen they were the highest (90%). Moreover, because ground nests were more exposed than real grouse nests due to the lack of a camouflaging, incubating hen and scent cues, the ratio of ground-to-pole-nest predation exaggerated the relative predation exerted by birds (e.g., Storaas 1988, Willebrand & Marcström 1988).

Our modeling approach identified habitat type as the main factor affecting predation rates in Pinega, where egg loss varied more between habitat types in both ground and pole nests than in Varaldskogen. This difference between the two areas may result from different predator guilds. Varaldskogen is dominated by generalist predators (Red Fox, Badger and Eurasian Jay), whereas in Pinega predators are habitat specialists (Red Squirrel, Pine Marten and Siberian Jay), all associated with old coniferous forest (Andrén & Delin 1994, Brainerd & Rolstad 2002, Eggers *et al.* 2005, Gienapp & Merilä 2011). The two landscapes also differ structurally: Pinega hosts large expanses of old forest separated by large open bogs, whereas Varaldskogen consists of 4–20 ha units of managed forests of different ages. While the Siberian Jay avoids open areas, the Eurasian Jay in Varaldskogen readily flies across narrow open patches. Moreover, open areas in Pinega consisted almost exclusively of open, grassy bogs, as opposed to 1–5 years-old clear-cuts in Varaldskogen. The bogs in Pinega may have provided less food for the Pine Marten than the recent clear-cuts in Varaldskogen, which in turn may have reduced the movements of this mammalian predator in the former area. Hence, the different spatial arrangements of habitat types, combined with differ-

ent predator guilds, to a large extent explain why nest predation varied more with habitat in Pinega than in Varaldskogen.

Contrary to Pinega, predation varied in Varaldskogen mainly with canopy cover and less with habitat type, as also found for spruce plantations in Norway (Einarsen *et al.* 2008). In Varaldskogen, ground nests with higher canopy cover survived better than those with less cover in all habitat types. This may be explained by the cyclic fluctuations and habitat distribution of microtine rodents – the preferred food of Red Fox (Wegge & Storaas 1990). The two main rodent species – Bank Vole *Myodes glareolus* and Field Vole *Microtus agrestis* – both peaked during the year of the present study (P. Wegge, unpubl. data). The former species is mainly associated with bilberry-rich, mature forest and the latter with grassy clear-cuts – both with relatively low canopy cover. During the study year, the Red Fox may have preferentially hunted in these two types of habitat, leading to more frequent encounters with artificial nests there than in the other types of habitat. In Pinega, rodent cycles have virtually disappeared during the last 10–15 years (Pinega State Reserve, unpubl. data) and have therefore not affected the foraging pattern of predators.

The observed dependence of predation on canopy cover also suggests that aerial avian predators – such as Hooded Crow and Raven – might have been more important than their low abundances implied. If so, it suggests that nest predation is a complex process and governed by factors other than visibility and abundance (Pelech *et al.* 2010). These authors concluded that learning and behaviour could account for most of the variation in nest predation. Similarly, Eggers *et al.* (2008) showed that parental activity near the nest may markedly increase the predation rate on nests of the Siberian Jay. Moreover, Huhta *et al.* (1996) reported a lack of correlation between predation and visibility of artificial nests in Finland.

As indicated by the present study and Storaas and Wegge (1987), predation on real Capercaillie and Black Grouse nests is relatively high in Varaldskogen, and breeding success, i.e., the number of chicks per female in August, is reportedly lower there than in Pinega (Borchtchevski *et al.* 2003, Wegge & Rolstad 2011). However, in spite of this difference in net reproductive output, popu-

lations of both species have remained relatively stable in both study areas for more than a decade (Wegge & Rolstad 2011, Pinega State Reserve, unpubl. data). These findings indicate that the mortality of fledged chicks and/or adult birds is higher in Pinega, and that this demographic trait may play a more important role in regulating populations there than in Varaldskogen. The Goshawk, a major predator on adult forest grouse, is common in Pinega (Borchtchevski *et al.* 2003), which supports this inference.

The present study uncovered differences between two study areas in predation of artificial nests, which could be explained mainly by different predator guilds and compositions of landscapes. The comparison of predation rates on ground and pole nests provided tentative evidence for the relative significance of different avian and mammalian predators. Nevertheless, the lack of clearer relationships between predation rate and some environmental variables, especially nest concealment in different habitat types, confirmed that nest predation involves behavioural components, which needs to be taken into consideration in the design of nest-predation studies.

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Metsäkanalintujen pesiin kohdistuva lintu- ja nisäkäspetojen saalistus kahdella borealisella metsäalueella keinopesien valossa

Munien saalistus on tärkeä metsäkanalintujen pesimämenestystä määrittävä tekijä, mutta nisäkäs- ja lintupetojen roolit tunnetaan tässä suhteessa huonosti. Kevään ja alkukesän 2010 aikana tutkittiin maahan ja 1,5 m korkeiden tolppien päähän asetettuihin keinopesiin kohdistuvaa saalistusta intensiivisen metsätalouden pirstomalla (Varaldskogen, Norja) sekä luonnontilaisella metsäalueella (Pinegan metsiensuojelualue, Luoteis-Venäjä). Tolppapesät mittasivat lintu- ja maapesät sekä lintu- että nisäkäspetojen vaikutusta. Pesäsaalistus

oli merkitsevästi korkeampi Varaldskogenissa kuin Pinegassa, ja maapesiin kohdistui 2,5-kertainen saalistus tolppapesiin verrattuna. Pinegassa saalistus pesätyyppien välillä oli samanlaista.

Tutkimusalueiden välinen ero johtui luultavasti erilaisista saalistajakilloista: nisäkäsgeneralistit, kuten kettu ja mäyrä, olivat tavallisia Varaldskogenissa mutta harvinaisia Pinegassa. Latvuspeitto selitti valtaosan saalistuksessa havaitusta vaihtelusta Varaldskogenissa mutta ei Pinegassa. Tolppapesiin kohdistuva saalistus vaihteli samalla tavoin eri ympäristöissä tutkimusalueiden sisällä, toisin kuin maapesiin kohdistuva saalistus.

Koska korppi (*Corvus corax*) ja varis (*Corvus corone cornix*) olivat harvinaisia tai puuttuivat, havainto viittaa siihen, että närhellä (*Garrulus glandarius*) Varaldskogenissa ja kuukkelilla (*Perisoreus infaustus*) Pinegassa näytti olleen yhtä tehokas pesien löytämis- ja saalistuskyky. Vaikka koejärjestely salli lintu- ja nisäkäspetojen vaikutusten vertailun, saalistuksen ja tiettyjen tutkittujen muuttujien välillä olevien selkeämpien riippuvuuksien vähyys viittaa siihen, että pesäsaalistus on monimutkainen prosessi, johon liittyvät petojen käyttäytymispiirteet.

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