

Capercaillie broods in pristine boreal forest in northwestern Russia: the importance of insects and cover in habitat selection

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Abstract: Capercaillie (*Tetrao urogallus* L., 1758), the largest and most size-dimorphic species of grouse, is decreasing in number throughout its man-modified range in the boreal forests of the Palaearctic. Poor reproduction owing to direct and indirect effects of commercial forestry is considered a main cause of the decline. We studied brood habitats in a pristine forest in northwestern Russia to identify key elements in habitat selection in the natural environment of this species. We monitored the movement of 10 radio-marked broods during their first 7 weeks of life, and compared the abundance of insects and cover at their locations ($N = 120$) with nearby random control sites. The broods preferentially used moist spruce forest and the insect-rich herb spruce forest, but were most often located in the more abundant Vaccinium spruce forest, which was richest in bilberry (*Vaccinium myrtillus* L.) and associated lepidopteran larvae. Brood locations were consistently richer in insects than random controls in 3 of the 4 habitat types studied. The most pronounced difference was in the density of lepidopteran larvae, a food source known to form an important part of the diet of young capercaillie chicks. Broods continued to select insect-rich sites throughout the 7 week age period; in the preferred moist spruce forest, larval abundance increased at brood locations, while it remained constant at control sites. Compared to the distribution of insects, cover did not appear to be as an important determinant of brood habitat selection, possibly because the structural characteristics were rather similar among the most widely used habitat types. Shrub cover tended to be higher at brood locations than at controls, whereas vertical cover along the ground was not different. This relationship to cover factors may reflect an adaptation to avoid predation by goshawk (*Accipiter gentilis* L., 1758), the most important predator of grouse in this pristine boreal forest.

Résumé : Les nombres de grands tétras (*Tetrao urogallus* L., 1758), l'espèce de tétraoniné qui possède la plus grande taille et le plus fort dimorphisme sexuel, sont en régression dans toute leur aire de répartition affectée par les humains dans les forêts boréales de la région paléarctique. L'insuccès de la reproduction relié aux effets directs et indirects de l'industrie forestière est considéré comme la cause principale de ce déclin. Nous avons examiné les habitats de nidification dans une forêt vierge du nord-ouest de la Russie afin d'identifier les éléments essentiels de leur sélection d'habitat dans leur environnement naturel. Nous avons suivi les déplacements des petits de 10 couvées porteurs d'émetteurs radio durant les 7 premières semaines de leur vie et nous avons comparé l'abondance des invertébrés qui leur servent de nourriture ainsi que l'importance de la couverture végétale dans les sites utilisés ($N = 120$) et dans des sites témoins situés à proximité et choisis au hasard. Les petits utilisent de préférence la forêt humide d'épinettes et la forêt herbeuse d'épinettes qui est la plus riche en insectes; ils se retrouvent cependant le plus souvent dans la forêt abondante d'épinettes et de *Vaccinium* qui est la plus riche en myrtilles (*Vaccinium myrtillus* L.) et en larves de lépidoptères associées. Les sites choisis par les petits de ces couvées sont constamment plus riches en invertébrés que les sites sélectionnés au hasard dans 3 des 4 types d'habitat étudiés. La différence la plus marquée est celle de la densité des larves de lépidoptères, une source de nourriture qu'on sait former une partie importante du régime alimentaire des oisillons du grand tétras. Les petits continuent à sélectionner des sites riches en insectes tout au long de la période de 7 semaines. Dans la forêt humide d'épinettes, un habitat recherché, l'abondance des insectes augmente aux sites choisis par les petits, alors qu'elle demeure constante aux sites témoins. Par comparaison avec la répartition des insectes, la couverture végétale ne semble pas être un facteur déterminant aussi important de la sélection d'habitat, peut-être parce que les caractéristiques structurelles sont plutôt semblables dans les types de forêts les plus utilisés. La couverture de buissons tend à être plus importante aux sites choisis par les petits que dans les sites témoins, alors que la couverture verticale au sol n'est pas différente. Cette relation avec les facteurs de la couverture végétale peut être le reflet d'une adaptation pour

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éviter la prédation par l'autour des palombes (*Accipiter gentilis* (L., 1758)), le plus important prédateur des tétraonidés dans cette forêt boréale vierge.

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Introduction

The large and highly size-dimorphic capercaillie (*Tetrao urogallus* L., 1758) has a wide distribution in the boreal forests of the Palaearctic, from Norway in the west to Lake Baikal in Russia in the east. Small, isolated populations also exist in central European mountain forests and in Scotland (Johnsgard 1983). Numbers have declined throughout its range during the past decades, presumably because of direct and indirect effects of commercial forestry (Storch 2000). Being most abundant in older, natural forests (Seiskari 1962), the causes of the general decline have been attributed to loss and fragmentation of the preferred habitat (Wegge et al. 1992; Storch 1995). In Scotland, factors related to increased rainfall owing to climatic change have been put forth as an explanation for their poor reproduction in recent years (Moss et al. 2001).

No comprehensive study has identified the demographic components associated with the general population decline of capercaillie. With its wide geographical distribution across different forest and climatic regions, main causes of local declines are likely to vary. However, studies in Finland (Kurki et al. 2000), Germany (Storch 1994), Scotland (Moss 1994), and Norway (Storaas and Wegge 1987; Wegge et al. 1990) have provided indirect evidence that the decline is caused by increased loss of eggs and chicks. Higher losses of chicks may be due to the lack of optimal food quality or elevated chick predation pressure, the latter either facilitated through higher predator abundance (Henttonen 1989) or more efficient predator-search in forestry-modified landscapes (Storaas et al. 1999).

The capercaillie is mostly ground dwelling, and shortly after hatching, the precocial chicks leave the nest. During their first weeks of life, they are in need of easily digestible and nutritious insect food, as their intestinal caeca are not yet developed to use plant foods efficiently (Rajala 1959; Moss and Hanssen 1980). Insects are rich in amino acids such as cysteine and methionine, which are assumed to be important for chick growth and survival. Thus, insects dominate the diet of young grouse chicks (Moss and Hanssen 1980; Savory 1989). Insects comprise more than 50% of the diet of capercaillie during the first 4 weeks of life (Rajala 1959; Kastdalen and Wegge 1985; Spidsø and Stuen 1988). During this early period, broods prefer old, moist habitat types that are dominated by ericaceous shrubs (Børset and Krafft 1973; Wegge et al. 1982; Rodem et al. 1984; Storch 1994), which support a large number of insects (Stuen and Spidsø 1988; Biedermann 1992), especially lepidopteran larvae associated with bilberry (*Vaccinium myrtillus*) shrubs (Kastdalen and Wegge 1985; Atlegrim and Sjöberg 1995; Picozzi et al. 1999). Broods tend to switch to forb-dominated habitat types as they grow older (Rodem et al. 1984), at which stage plants dominate their diet.

Most studies of capercaillie brood habitats were conducted in Europe, where the forests have been modified by

human activities. In this study, we explored habitat use by broods in a Russian pristine boreal forest, which is the natural habitat of this species. Because insects are quite important for the growth of grouse chicks (Savory 1989) and because survival of capercaillie chicks appears to correlate positively with insect abundance (Picozzi et al. 1999), we sampled the abundance of insects in different habitat types to assess the role of this food category in the broods' use of habitats. Like in other species of grouse, cover that minimizes predation is also likely to be important in brood habitat selection (Johnsgard 1983; Bergerud and Gratson 1988). With increasing age, insects become less important in the diet of chicks. Thus, we examined the relationship between habitat use and insect abundance and cover as the broods grew older.

Methods

Study area

The study was conducted in the 298 km² Pinega (Pinezshkiy) Nature Reserve in the Archangelsk region of northwestern Russia (64°42'N–64°25'N, 42°67'E–43°11'E), which is located on the southeastern part of the Belomoro–Kuloyskoe Plateau in the northern taiga subzone. The study area has a gentle topography with altitudes between 50 and 150 m above sea level. The climate is continental, with mean temperatures of 14.3 °C in July and –14.7 °C in January. Snow covers the ground from late October to mid-May.

The main reason for protecting the area was the special bedrock features, consisting of limestone and karst formations. The area is flat with a high groundwater level. Along with nutritious bedrock, small variations in topography have led to a mosaic and fine-grained mixture of habitat types, consisting of a mixed, old coniferous forest dominated by spruce (*Picea* spp.) intermixed with Scots pine (*Pinus sylvestris*) and Siberian larch (*Larix sibirica*). Trees more than 120 years old dominate the overstory, while the understory is approximately 40–60 years old. Some patches are dominated by Scots pine and Siberian larch in the tree layer, whereas spruce generally dominates the lower strata. Bogs and lakes cover approximately 11%, mainly located in the western part of the reserve (Puchnina et al. 2000). About 21% of the reserve has been affected by natural forest fires. Following such disturbance, birch (*Betula* spp.) and aspen (*Populus tremula*) have become the dominant plant species during the regrowth phase of the forest.

The fauna is typical of undisturbed, northern boreal forests. Of the four tetraonids, hazel grouse (*Bonasa bonasia* (L., 1758)) is the most numerous, followed by capercaillie, black grouse (*Tetrao tetrix* (L., 1758)), and willow ptarmigan (*Lagopus lagopus* (L., 1758)). Autumn density of capercaillie is approximately 6/km², and the main grouse predators are the goshawk (*Accipiter gentilis* (L., 1758)) and European pine marten (*Martes martes* (L., 1758)). Red fox (*Vulpes*

vulpes (L., 1758)) are nearly absent within the reserve (Borchtchevski et al. 2003).

Telemetry

Capercaillie hens were captured and radio-marked with 28 g transmitters in the 142 MHz frequency range at three neighbouring leks in May. We tracked nine hens with broods, four in 2000 and five in 2001. One brood was monitored in both years; the others were all different broods. In addition, we radio-marked one hen with a brood in July 2001 at brood age of approximately 5 weeks.

We located broods with a receiver and a hand-held, directional antenna. The approximate position of the hen was first ascertained from a distance of 200–300 m. The brood was then located by walking around it within a distance of 25–30 m. It was possible to determine the brood's position visually by comparing the compass bearings from at least three points. We used global positioning satellite data to locate the tracking points and returned the following day to investigate the habitat.

In 2000, broods were located at irregular intervals until 6 August, at a mean brood age of approximately 6 weeks (4 broods, $N = 46$ locations). In 2001, six broods were located 64 times, up to mean age of approximately 7 weeks. To avoid autocorrelation, no broods were located at shorter intervals than 6 h; most intervals (92%) were >24 h (median for all broods = 68 h). Ten locations of unmarked broods, flushed during fieldwork in 2001, were also recorded and examined in the same way. Thus, 120 locations were recorded, spread almost equally across brood age until 7 weeks of age.

Habitat and insects

Habitat types were identified and described by V. Borchtchevski (personal communication) based on a vegetation map prepared by Saburov (1988). Two types — *Pinetum cladinosum* and *Piceetum menyanthosum* — covered small areas mainly outside the study area and were excluded. The study area consisted of four main habitat types. Their spatial coverages and floristic characteristics are given in Table 1.

We estimated the availability of habitat types, according to a nonmapping technique described by Marcum and Loftsgaarden (1980), by sampling 100 points, spaced 200 m apart, along random transects within the approximately 30 km² area used by the radio-marked broods. Habitat type was assigned at each point. At brood locations, we recorded habitat type and also habitat characteristics within circular plots of 10 m radius. We also examined similar-sized plots near the brood locations to learn if broods made selections on a small spatial scale. These controls ($N = 120$) were in a random direction 50 m from the center of the brood locations. Because of the fine-grained mosaic of habitat types, approximately 1/3 of these plots fell in a different type than that of the brood location (termed DT plots). Thus, although the controls were not located independently of where the broods were, they probably described the characteristics of the various habitats within the area. This was confirmed when we compared the characteristics of DT plots with that of the other controls within the same habitat types; there were no differences in floristic or insect compositions between these two categories of controls within any of the four

habitat types (Wilcoxon's signed-rank and paired t tests, all p values > 0.05). Thus, we considered all control plots as representative of the habitat characteristics of the 30 km² study area (i.e., they described what was available for the broods). In most analyses, we used data from all control plots; only in paired tests between brood locations and controls within the same habitat types were DT plots excluded.

We recorded the following data at brood locations and control plots:

1. Ground layer: Horizontal cover, estimated visually to the nearest 5%, of species of graminoids, herbs, and ericaceous shrubs up to 0.5 m tall.
2. Shrub layer: Horizontal cover, estimated visually to the nearest 5%, of tree and shrub species between 0.5 and 3 m tall. Branches and stems of taller trees within this interval were also included.
3. Tree layer: Horizontal cover, estimated visually to the nearest 5%, of tree species >3 m tall.
4. Vertical cover along the ground: To assess cover against ground predators, we used a method developed by Finne et al. (2000) where we estimated the longest distance in metres that a fox head would be visible from the center of the plot 30 cm above the ground. The measurement was made in the eight cardinal directions and averaged. Obstructions by rocks, windfalls, tree stems, and anthills along the ground were included in this measurement.
5. Insects: A circular net of 25 cm radius on a 2 m pole was swept across a 3 m distance in the ground layer, with 10 sweeps per plot. Captured insects >1.5 mm long were saved and later identified at the Norwegian University of Life Sciences, Ås, based on preserved samples, pictures, and explanations provided by Sundby (1970). If the vegetation was wet, sweep-net sampling was postponed until it had dried to ensure standard field conditions for comparisons. Sweep netting provides a good measure of insects in the "arboreal" part of the ground layer, but grossly underestimates the abundance of ants, which may compose a significant part of the chicks' diet (Stuen and Spidsø 1988).

We compared data collected during the first 4 weeks post hatch with that collected during the following 3 weeks of brood age to examine if habitat use changed over time. We split the data at this age because earlier studies have shown that plants begin to dominate the diet after the chicks are 4 weeks old (Rajala 1959; Kastdalen and Wegge 1985).

Results

Use of habitat types

Broods used moist spruce forest and herb spruce forest more often than expected based on availability (χ^2 tests followed by Bonferroni z tests, $P < 0.05$ and $P < 0.10$, respectively; Fig. 1). *Vaccinium* spruce forest, the most common type, was used less than expected in 2001 and when data from both years were pooled ($P < 0.05$). Pine bog was avoided in 2000 ($P < 0.05$), but not significantly in 2001 or when data from both years were pooled ($P \geq 0.1$).

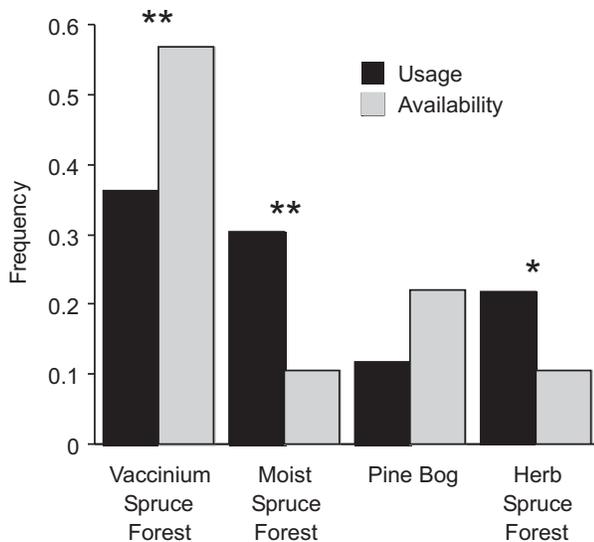
There was no difference in use of habitat types between years ($\chi^2_{[3]} = 4.72$, $P = 0.19$), or between the first 4 weeks and the next 3 weeks post hatch ($\chi^2_{[3]} = 2.08$, $P = 0.56$) when the data from both years were pooled.

Table 1. Characteristics of forest types within the study area used by capercaillie (*Tetrao urogallus*) in the Pinega Forest Reserve, northwest Russia.

Habitat type	Russian classification	Relative area (%)	Characteristics
Vaccinium spruce forest	<i>Piceetum myrtillosum</i>	54	Tree layer: <i>Picea</i> spp., <i>Larix sibirica</i> , <i>Pinus silvestris</i> , <i>Betula</i> spp., <i>Populus tremula</i> ; shrub layer: <i>Picea</i> spp., <i>Betula</i> spp., <i>Juniperus communis</i> , <i>Salix</i> spp.; ground layer: <i>Vaccinium myrtillosum</i> , <i>Vaccinium uliginosum</i> , <i>Vaccinium vitis-idaea</i> , <i>Melampyrum sylvaticum</i>
Moist spruce forest	<i>Piceetum polytrichosum</i>	10	Tree layer: <i>Picea</i> spp., <i>Betula</i> spp.; shrub layer: <i>Picea</i> spp., <i>Betula</i> spp., <i>Salix</i> spp., <i>Sorbus aucuparia</i> ; ground layer: <i>V. myrtillosum</i> , <i>V. uliginosum</i> , <i>Rubus chamaemorus</i> , <i>Equisetum</i> spp., <i>Melampyrum</i> spp., <i>Trollius europaeus</i> , <i>Dryopteris</i> spp.
Herb spruce forest	<i>Piceetum geranium</i>	10	Tree layer: <i>Picea</i> spp., <i>L. sibirica</i> , <i>P. tremula</i> , <i>Betula</i> spp.; shrub layer: <i>Picea</i> spp., <i>L. sibirica</i> , <i>Betula</i> spp., <i>P. tremula</i> , <i>Salix</i> spp., <i>Rosa acicularis</i> , <i>S. aucuparia</i> ; ground layer: <i>Geranium sylvaticum</i> , <i>Trientalis europea</i> , <i>Crepis paludosa</i> , <i>Majenthemum bifolium</i> , <i>Vicia sylvatica</i> , <i>Athyrium filix-femina</i> , <i>Dryopteris</i> spp., <i>Gymnocarpium dryopteris</i> , <i>V. myrtillosum</i>
Pine bog	<i>Pinetum sphagnosum</i>	21	Tree layer: <i>P. sylvestris</i> , <i>Betula</i> spp.; shrub layer: <i>P. sylvestris</i> , <i>Betula</i> spp.; ground layer: <i>V. uliginosum</i> , <i>V. vitis-idaea</i> , <i>R. chamaemorus</i> , <i>Chamaedaphne calyculata</i> , <i>Ledum palustre</i> , <i>Andromeda polifolia</i> , <i>Eriophorum vaginatum</i>
Others		5	Mainly open peat bogs and lichen pine forest

Note: Authority names for plant species are as follows: *Picea* A. Dietr., *Larix sibirica* Ledeb., *Pinus silvestris* L., *Betula* L., *Populus tremula* L., *Juniperus communis* L., *Salix* L., *Vaccinium myrtillosum* L., *Vaccinium uliginosum* L., *Vaccinium vitis-idaea* L., *Melampyrum sylvaticum* L., *Sorbus aucuparia* L., *Rubus chamaemorus* L., *Equisetum* L., *Melampyrum* L., *Trollius europaeus* L., *Dryopteris* Adans., *Rosa acicularis* Lindl., *Geranium sylvaticum* L., *Trientalis europea* L., *Crepis paludosa* (L.) Moench., *Majenthemum bifolium* L., *Vicia sylvatica* L., *Athyrium filix-femina* (L.) Roth, *Gymnocarpium dryopteris* (L.) Newman, *Chamaedaphne calyculata* (L.) Moench, *Ledum palustre* L., *Andromeda polifolia* L., and *Eriophorum vaginatum* L.

Fig. 1. Distribution of locations of capercaillie (*Tetrao urogallus*) broods ($n = 10$) post hatch until 7 weeks of age in different habitat types (data pooled for 2000 and 2001), and the proportions of same habitat types within the area used by the broods (**, $P < 0.05$; *, $P < 0.10$).



It was not possible to compare individual habitat use statistically, because some broods were located only a few times. Instead, we compared the habitat distribution of the brood located most often ($n = 58$) with that of the rest of the broods pooled ($n = 68$). Their distributions did not differ

($\chi^2_{[1]} = 3.23$, $P = 0.199$). This brood was monitored in both years. Its use of habitats did not vary between years ($\chi^2_{[1]} = 1.13$, $P = 0.291$).

Habitat characteristics

Ground layer

Cover of ericaceous shrubs, particularly bilberry, was higher in vaccinium spruce forest than in any of the others, and herbs were most abundant in the herb spruce forest (Table 2). Between the two bilberry-dominated habitat types, bilberry was twice as abundant in vaccinium spruce forest than in the preferred moist spruce forest. There were no differences in total cover between brood locations and controls in any of the four habitat types, except in the herb spruce forest where brood locations were in denser cover (paired t test, $t_{[16]} = 2.61$, $P = 0.019$; Table 2).

Shrub and tree layers

Except for the more open pine bog, there were no differences in total shrub or tree cover among the other three habitat types. However, shrub cover was higher at brood locations than in controls in all habitat types pooled (Wilcoxon's signed-rank test, $W = 447.0$, $P = 0.048$, $n = 60$; Fig. 2), with the most pronounced difference being in the moist spruce forest (paired t test, $t_{[9]} = 1.88$, $P = 0.093$; Table 2). There was also a tendency for higher tree cover at brood locations than in controls in this habitat type (paired t test, $t_{[9]} = 1.680$, $P = 0.128$).

Table 2. Horizontal cover (%) and sighting distance (m) along the ground at brood locations of capercaillie and at control plots in four habitat types in the Pinega Forest Reserve, northwestern Russia, during June–July 2000 and 2001.

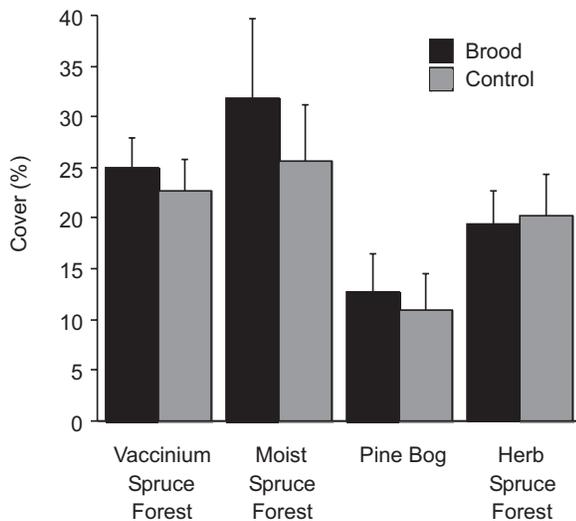
	Vaccinium spruce forest		Moist spruce forest		Herb spruce forest		Pine bog	
	Brood	Control	Brood	Control	Brood	Control	Brood	Control
Ground layer								
Bilberry	17.0	17.5	8.0	7.0	0.0	1.0	0.0	0.0
Other ericaceous shrubs	21.8	18.2	9.7	7.9	4.0	5.0	14.1	9.0
Others*	2.5	5.6	23.1	24.1	64.6	49.0	18.1	20.7
Total ground layer	41.3	41.3	40.8	39.0	68.6	55.0	32.2	29.7
Shrub layer								
	25.5	23.3	34.0	26.5	19.9	19.9	12.7	11.0
Tree layer								
	34.9	34.8	40.7	34.4	30.2	31.0	19.8	19.9
Sighting distance†								
Age 1–4 weeks	12.2	11.9	11.1	10.9	8.9	9.7	14.9	17.7
Age 5–7 weeks	8.9	10.3	7.5	6.9	6.5	7.9	—	—

Note: Values are the arithmetic means and medians (in italics). Paired values in boldface type denote significant differences at $P < 0.05$.

*Mainly herbs.

†Refer to the text for a description of sighting distance along the ground (equal to vertical cover).

Fig. 2. Mean (+90% confidence interval) percent shrub cover at brood locations of capercaillie and at control plots in different habitat types.



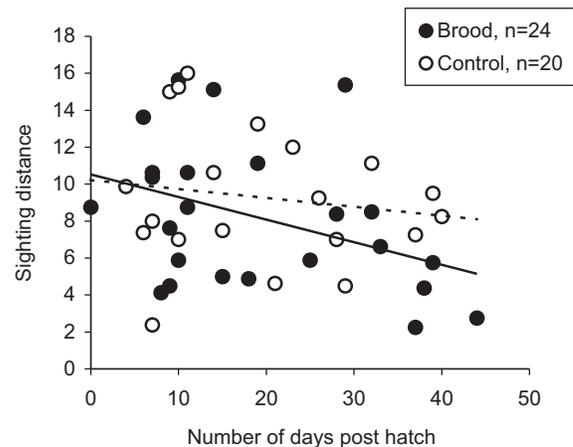
Vertical cover along the ground

Vertical cover, measured by the sighting distance along the ground, differed between habitat types (ANOVA on ranked data, $H = 15.0$, $P = 0.0019$, $df = 3$), mainly because there was less cover in the pine bog (Bonferroni correction, $P < 0.05$), with no differences among the other three types. There were no differences in vertical cover between brood locations and controls in any of the four habitat types (Table 2).

Changes during the brood period

The cover of bilberry in vaccinium spruce forest remained constant at brood locations during the 7 week period, but it decreased in the controls ($R = -0.296$, $P = 0.037$, $n = 38$). In all four habitat types, total cover of shrubs and trees remained constant at both brood locations and controls (all P val-

Fig. 3. The relationships between sighting distance along the ground and brood age at brood locations of capercaillie ($Y = 10.5 - 0.122X$, $P = 0.056$) and random control plots ($Y = 10.2 - 0.048X$, $P = 0.518$) in herb spruce forest.



ues > 0.32). Vertical cover did not follow the same pattern. Instead, sighting distance along the ground decreased (denser habitat) both at brood locations ($R = -0.395$, $P < 0.001$, $n = 107$) and at controls ($R = -0.263$, $P < 0.001$, $n = 107$) when data from all four habitat types were pooled. The patterns varied among habitat types: in pine bog and moist spruce forest, sighting distance decreased at both sites ($P < 0.10$); in vaccinium spruce forest, it remained constant at both sites; and in herb spruce forest, it remained constant at control sites, but decreased at brood locations ($P < 0.056$; Fig. 3), indicating that older broods selected denser cover at small spatial scales in this habitat type.

Distribution of insects

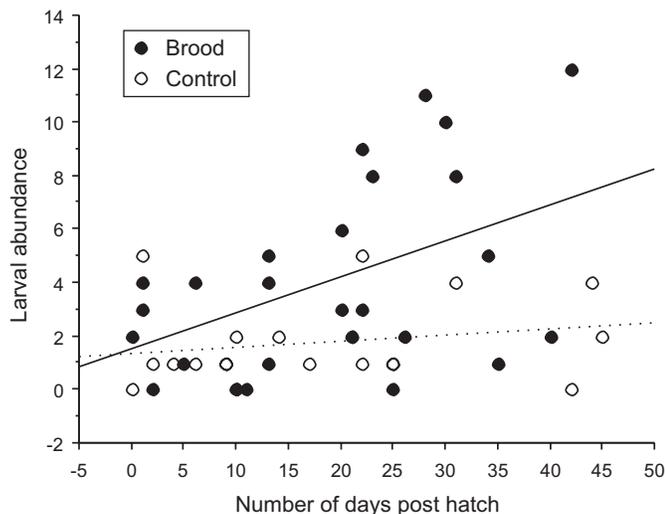
Total number of insects was highest in herb spruce forest (ANOVA on ranked data followed by Bonferroni correction, $P < 0.05$), mainly because of the presence of many two-

Table 3. Number of insects per 10 sweeps at brood locations of capercaillie and in control plots in different habitat types.

	Vaccinium spruce forest		Moist spruce forest		Herb spruce forest		Pine bog	
	Brood	Control	Brood	Control	Brood	Control	Brood	Control
Lepidopteran larvae	4.93	4.74	4.08	1.75	2.60	2.24	2.25	2.20
	$T = 1121, P = 0.78$		$T = 368.5, P = \mathbf{0.03}$		$T = 320.5, P = 0.95$		$T = 109.5, P = 0.74$	
Other insects	11.7	9.1	16.5	10.5	28.2	23.2	18.8	10.7
	$T = 1282.5, P = 0.13$		$T = 414, P = 0.21$		$t = 0.51, P = 0.46$		$T = 87, P = \mathbf{0.07}$	
Totals	16.5	14.0	20.6	12.2	30.8	25.4	21.0	12.9
	$T = 1226, P = 0.38$		$T = 383, P = \mathbf{0.06}$		$t = 0.76, P = 0.50$		$T = 89, P = \mathbf{0.09}$	

Note: The values represent the pooled 2000 and 2001 data. P values in boldface type are statistically significant at $P < 0.10$. (Mann–Whitney ranked-sum test (T) and paired t tests).

Fig. 4. The relationships between larval abundance and brood age at brood locations of capercaillie ($Y = 1.59 + 0.137X, P = 0.019$) and random controls ($Y = 1.27 + 0.0198X, P = 0.409$) in moist spruce forest.



winged flies (Diptera) and true bugs (Hemiptera), but lepidopteran larvae were most common in vaccinium spruce forest (Table 3). Total number of insects was higher at brood locations than in control plots in all habitat types. This difference was significant in the preferred moist spruce forest both in terms of total density of insects (Mann–Whitney ranked-sum test, $T = 383, P < 0.06$) and of number of larvae ($T = 368.5, P < 0.03$); the latter being more than 2 times more abundant at brood locations than at controls (Table 3). In the most widely used vaccinium spruce forest, the density of larvae was similar to that at brood locations in moist spruce forest, with no difference between brood locations and controls (Table 3).

When data from both years were pooled, the numbers of larvae in control plots in the preferred moist spruce forest remained constant ($P > 0.4$) during the 7 week age period, while they increased significantly at the brood locations in this habitat type ($P < 0.02$) (Fig. 4), with a significant difference in the b coefficients (slopes) of their regressions ($t_{144} = 1.86, P < 0.070$). Such diverging relationships were not detected in any of the other habitat types. In herb spruce forest, the total number of insects increased both at brood locations ($R = 0.339, P = 0.156$) and at controls ($R = 0.466, P < 0.069$),

whereas the opposite pattern was seen in pine bog (brood locations: $R = -0.778, P = 0.008$; controls: $R = -0.109, P = 0.764$). In vaccinium spruce forest, numbers of lepidopteran larvae and other insects did not change at brood locations or at controls during the 7 week period.

Covariation between insects and cover

There were no significant relationships between the abundance of insects and the densities of the ground, shrub, or tree layers. Applying linear and curvilinear regressions, including second degree polynomial, of densities of lepidopteran larvae, other insects, and total insects in the control plots on cover densities in each of the three layers provided no relationships (all tests, $P > 0.20$). Furthermore, there were no differences in lepidopteran larval or other insect numbers between the lowest one-third and the highest one-third intervals of shrub densities (unpaired t test for lepidopteran larvae and other insects, both P values > 0.18).

Discussion

Moist spruce forest and herb spruce forest were the preferred habitat types. Except for both being moist habitats, they differed markedly in the composition and density of the ground layer; the former consisted of a mixture of ericaceous shrubs and herbs, whereas the latter was denser and was covered almost exclusively with herbs without ericaceous shrubs. The most common habitat — vaccinium spruce forest with the highest density of bilberry and lepidopteran larvae — was statistically avoided, but broods were most often located in this habitat.

Broods selected insect-rich sites, as there were consistently more insects at brood locations than at controls within all four habitat types. Although insects were most abundant in the herb spruce forest, lepidopteran larvae were twice as abundant in vaccinium spruce forest than in the other habitat types. Among insects, lepidopteran larvae are probably the most important food source for young broods (Kastdalen and Wegge 1985; Atlegrim and Sjöberg 1995; Picozzi et al. 1999). Selection for lepidopteran larvae was clearly confirmed in this study; brood locations contained more lepidopteran larvae than controls in all habitats, and differences in other insect groups were not as pronounced as they were for lepidopteran larvae. Furthermore, in the preferred moist spruce forest, lepidopteran larval abundance at brood sites

increased with brood age, whereas it remained constant at nearby controls.

There were more insects at sites where broods had been foraging the day before than at sites 50 m away. This indicates that broods do not exhaust local foods during foraging. Extensive movements, particularly in early life, are a common feature among grouse broods (North American grouse: Bergerud and Gratson 1988; European grouse: Robel 1969; Wegge et al. 1982; Barikmo et al. 1985; Erikstad 1985; Storch 1994; P. Wegge, unpublished data). Our result that broods leave insect-rich sites lends support for Sonerud's (1985) win-stay hypothesis, i.e., extensive movement has evolved among wader and grouse broods to minimize predation by raptors. The fact that goshawks, not mammalian carnivores, are the main predators of grouse in this study area (Borchtchevski et al. 2003) further supports the above hypothesis.

Lepidopteran larvae are associated with ericaceous shrubs, particularly bilberry, which serve as host plants (Atlegrim 1991). Why then was vaccinium spruce forest, the habitat with the greatest abundance of bilberry and larvae, avoided? Statistical avoidance does not indicate that this habitat was unsuitable, as nearly 40% of all brood locations were recorded in this habitat type. The lack of greater use may be explained by the relatively low quality of plant foods available in vaccinium spruce forest compared with the other two statistically preferred spruce habitats. Vaccinium spruce forest contained virtually no herbs, whereas the ground layer in moist spruce and herb spruce forests consisted of >50% forbs. As chicks grow older and their daily food intake increases, the emerging and growing forbs are probably more nutritious and digestible than new leaves of ericaceous shrubs. This may explain why moist spruce forest was the most selected habitat; it contained medium densities of bilberry and lepidopteran larvae (and broods most strongly selected larval sites there). At the same time this habitat was relatively rich in herbs. Search efficiency may also have played a role in the selection of moist spruce forest. Atlegrim and Sjöberg (1995) reported that capercaillie chicks used lepidopteran larvae to a larger extent in wet spruce forest because they were able to search this habitat more efficiently because of the lower density of bilberry. The weak statistical preference for herb spruce forest may have been due to its rich abundance of other insects other than lepidopteran larvae and its high abundance of nutritious forbs.

With plants becoming more important in the chicks' diet with age, selection for insect-rich habitats was expected to diminish and to be replaced with habitats richer in plant foods. Such a pattern was not detected. The most likely explanation is that the period of observation was restricted to 7 weeks. Inference on the importance of insects has mainly been made based on the proportions of insects and plants in the diet. As chicks grow, their daily food intake increases. Thus, even though the proportion of insects relative to plants decreases with age, capercaillie chicks probably increase their intake of insects after 4 weeks of age. This is likely to be true for capercaillie chicks because of their remarkably fast growth rate (Linden 1981).

When food and cover habitats are quite different, animals may resort to spatial trade-offs by using each for different behaviours (Mysterud and Ims 1998). For highly mobile ani-

mals, trade-offs in habitat use are common even in coarse-grained landscapes. Among less mobile animals (i.e., grouse broods), trade-off is less likely to occur, because they forage while moving almost continuously during the 24 h cycle (P. Wegge, unpublished data). Instead, they probably select the best combination of food and cover among what is available, which appears to be the case in our study area. With the exception of pine bog, the three spruce-dominated habitat types were quite similar in structural characteristics and in food abundance. In the slightly preferred herb spruce forest, large amounts of cover in the ground layer, of nutritious forbs, and large numbers of insects other than lepidopteran larvae probably compensated for the lack of bilberry and associated lepidopteran larvae.

On a small spatial scale, the broods generally selected sites with high horizontal cover, whereas vertical cover along the ground was not higher at brood locations than at control sites. The selection for higher shrub cover but not for vertical cover probably reflects an adaptation against avian predators. In the study area, the red fox is nearly absent and the goshawk is the most important predator of forest grouse (Borchtchevski et al. 2003). Selecting dense shrub cover minimizes detection by goshawks; selection for vertical cover against ground predators may not have evolved to the same extent because of their lower importance for chick survival.

As the chicks grew older, horizontal cover in the three strata above the ground remained more or less constant both at brood locations and at controls. In contrast, vertical cover near the ground increased at both sites. This somewhat ambiguous result may be explained by brood foraging behaviour. Since there were no differences in vertical cover between sites of older broods and nearby controls, selection must have occurred on a larger spatial scale, i.e., older broods may have moved into areas that, in general, had more vertical cover. As chicks grow in size, bilberry leaves progressively constitute a larger fraction of their diet (Kastdalen 1986; Spidsø and Stuen 1988). Bilberry leaves in shaded growing sites contain less chemical defense against herbivory (Atlegrim 1991) and have greater nutritive quality (Hjeljord et al. 1990) than bilberry in more sun-exposed growing sites. Thus, selection for denser vertical cover may reflect selection for more access to higher quality bilberry vegetative food. That cover of bilberry did not decline at brood locations, while it did at the controls, in the widely used vaccinium spruce forest lends some support to this hypothesis. Furthermore, obstructions, which determine sighting distance, included anthills. In spruce-dominated forests, ants constitute an important part of the diet of capercaillie chicks (Kastdalen and Wegge 1985; Klaus et al. 1986; Spidsø and Stuen 1988; Picozzi et al. 1999). Storch (1994) found a strong correlation between brood habitat use, bilberry cover, and density of anthills, and suggested that ants provide a stable food source compared with other insects which fluctuate markedly in abundance because of weather. Predator avoidance behaviour may also be involved in that chicks are able to fly well after 4 weeks of age and a dense understory may increase their ability to escape pursuits by goshawks.

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