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The May diet of Capercaillie (*Tetrao urogallus*) in an extensively logged area of NW Russia

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The May crop contents of Capercaillie (*Tetrao urogallus*) from a highly disturbed (logged) area of NW Russia are documented for the first time. Plants of the tree-shrub layer and bog plants of the field layer together formed the main part of the diets of both cocks (75% of fresh weight) and hens (58%). Fragments of pine (*Pinus sylvestris*) and bilberry (*Vaccinium myrtillus*) were more abundant in crops of cocks, whereas hens consumed more young herbaceous shoots and track-side plants. Hens also garnered spruce seeds (*Picea* spp.) from tracks. Track-side food items formed up to a third of the diet of hens. These included shoots of clover (*Trifolium* spp.) and especially flower buds of coltsfoot (*Tussilago farfara*). Complete elimination of some forest tracks, as a management technique for Capercaillie, could result in a loss of food sources important to hens in most of their Eastern-European range. The closure of tracks from people and vehicles, and their conversion to habitat where spring-blooming plants for hens abundantly grow, seems a more viable conservation option. Even in a highly disturbed area, plants of the native taiga biotopes composed almost all the diet of cocks (ca. 97%). Compared to the cocks, the feeding strategy of hens was more opportunistic; hence, their spring diet may be less vulnerable to logging perturbations.

1. Introduction

Capercaillie (*Tetrao urogallus*) is a species associated with open, typically old forest, and in Northern Eurasia its range roughly coincides with the distribution of Scots pine (*Pinus sylvestris*), with its needles being Capercaillie main winter food, and bilberry (*Vaccinium myrtillus*), the principal Capercaillie diet during snowless periods (Borchtchevski 1986). Capercaillie have traditionally been hunted in much of their range and are sensitive to disturbance by humans (Storch 2000). Consequences of this sensitivity include long flushing distances (Thiel *et al.* 2007) and the avoidance by Capercaillie of woodland close to roads and tracks where people are likely to be encountered (Summers *et al.* 2007). As a means of reducing disturbance and increasing habitat for Capercaillie, destruction or closure of some segments of forest tracks and trails, and regulation of hiker numbers, have been recommended as management techniques (Summers *et al.* 2007, Thiel *et al.* 2007). These actions seem to positively affect Capercaillie (Scherzinger 2003). However, forest tracks probably are important as a source of grit, and in snowless periods, certain plant species growing at or adjacent to the tracks are an important source of food for Capercaillie (Lobatchev & Scherbakov 1936). This importance may be most pronounced in spring when grouse hens need emerging young

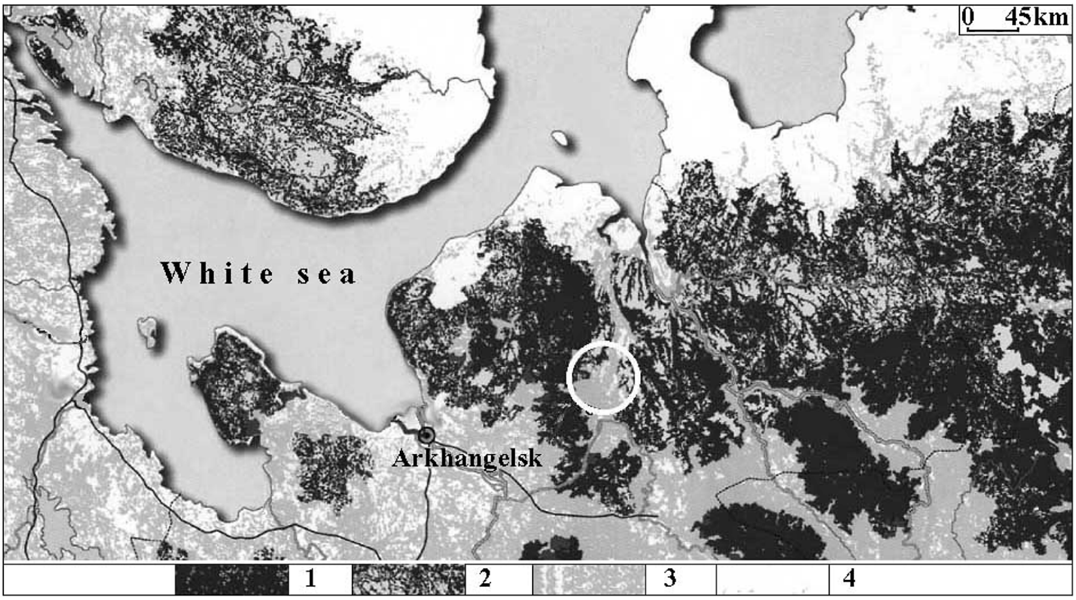

Fig. 1. The study area (white ring) relative to the native forest and bog-forest tracts in NW Russia. 1 – native forest, 2 – native bog forest, 3 – disturbed (logged) areas, 4 – treeless areas.

plants in their diet to lay high-quality eggs (Watson & Moss 2008). Snowless patches with early-emerging field-layer plants attract Capercaillie hens (e.g. Pulliainen & Tunkkari 1991), and in spring such patches occur earlier along tracks than within closed forest.

In NW Russia, the spring diet of Capercaillie has been studied only in undisturbed areas (Teplov 1947, Semenov-Tjan-Shanskiy 1960, Borchtchevski 1994a, 1995), and there is thus no information on this topic in managed forests for this region. Hence the aims of this paper were (1) to characterize the spring diet of Capercaillie in an extensively-logged area, and (2) to estimate the importance of track-side vegetation as Capercaillie food during the egg-laying period in spring.

2. Material and methods

2.1. Study area

The data were collected in northern Arkhangelsk, NW Russia, in an area of ca. 1,500 km^2 adjacent to the Pinega State Reserve (64°42' N, 42°67' E). The altitude in the study area ranges between 50 and 150 m a.s.l. The climate is continental, with mean temperature in July being +14.3° C and in January being –14° C. Total yearly precipitation is ca. 550 mm, and snow covers the ground from late October to mid-May. The area lies in the northern taiga sub-zone, with spruce (*Picea obovata*, *P. obovata* × *P. abies*) and Scots pine (*Pinus sylvestris*) as the dominant tree species.

The vegetation, however, resembles that of the central taiga sub-zone, due to the carbonated soils and karst relief. Larch (*Larix sibirica*) and honeysuckle (*Lonicera xylosteum*, *L. pallasii*) are common plants among other species of megatrophic habitats, including numerous legumes (Fabaceae). The forest has been extensively logged during the past 60–70 years, and currently the landscape consists of regenerating clear-cuts and secondary forests that occupy 55–70% of the area, while bogs cover approximately 15%. A network of sand-covered log-hauling tracks, the majority of which are currently unused, traverses the area. The fauna can be described as being typical for northern boreal forests.

The study area was located southwest from a little-perturbed, >10,000-km^2 tract of taiga (Fig. 1). According to transect counts, the spring densities of Capercaillie were estimated as 0.6 ind./km^2 on logged areas (Borchtchevski *et al.* 2006) and

Table 1. Numbers of Capercaillie crops studied, mean numbers of broken follicles in ovaries (Follicles), and mean proportion of snow-free ground in the study area (Snow free%) in 1999–2006.

Parameter	Year	May date					
		1–5	6–10	11–15	16–20	21–25	26–31
No. males	1999	–	1	4	–	–	–
	2000	3	–	–	–	–	–
	2001	3	–	–	2	4	5
	2002	3	–	–	–	–	–
	2004	–	1	2	–	–	–
	2005	–	1	1	–	–	–
	2006	–	1	2	2	5	–
	Total	9	4	9	4	9	5
No. females	1999	1	–	1	–	1	–
	2004	2	–	3	1	–	–
	2005	–	1	–	–	–	–
	2006	4	1	7	1	–	–
	Total	7	2	11	2	1	–
Follicles		1.2	3.0	4.4	6.0	11.0	–
Snow free (%)		14	55	87	59	86	98

ca. 2.0 ind/km^2 in unperturbed areas (V. Borchtchevski, unpubl. data). The local Capercaillie population thus apparently exceeds 20,000 individuals.

Based on the number of broken follicles in the ovaries of Capercaillie hens (Sleptsov 1948), the egg-laying period lasts throughout May (Table 1). The proportion of snow-free ground was calculated by means of visual estimates, made in each habitat type on an almost daily basis while traversing the study area on foot or by ski. On average, more than half of the area was snow-free, and thus available to egg-laying females for foraging, from the second pentad of May onwards (Table 1), although late snow falls often occurred until the first pentad of June.

2.2. Data collection and analysis

The data on Capercaillie crop content were mostly collected from aboriginal hunters with government permits for spring hunting, and to a lesser degree under a special authorization granted by the State Service of Game Management (for more details, see Appendix). The data were collected during 1–31 May of 1999–2006. Reliable data on Capercaillie spring diet would otherwise have been difficult to obtain, yet such information is essential for informed management decisions on the large network of logging tracks that are not used any more. Other assessment methods for spring diet – such as faecal analysis – have serious biases (see Discussion); hence it was essential to obtain crops for this study. Birds with empty crops were excluded from the data; thus, 40 males and 23 females were included in the analysis (Table 1). Almost a third of the cocks was shot at leks during early morning hours. The biggest number of Capercaillie hunted was in 2006 (23 ind./year, Table 1), which amounted less than 0.5% of the local population.

Crop contents were usually analyzed no later than 2–15 hours after the death of individuals. The contents were sorted and identified to the lowest taxonomic level possible, often to species; each was weighed to 0.1 g. Undetermined food fragments were stored in alcohol, or dried, for later identification. The amount of each type of food in the diet was expressed as the percentage of the total fresh weight of food in a crop, and Mann-Whitney *U*-test was used to evaluate differences between sexes in the proportions of particular types of food.

Table 2. Total and mean (± SD) fresh weight of food items and pieces of grit in Capercaillie crops collected from the Pinega district of the Arkhangelsk region during 1999–2006.

Parameter	Males (n = 40)	Females (n = 23)
Food, total (g)	1,176.1	634.2
Food, per crop (g)	29.4±45.6	27.6±35.3
Food, Mann-Whitney *U*-test	P = 0.966	
Grit, total (g)	1.8	2.3
Grit, mean fodder mass (%)	0.17±0.80	0.68±2.14
Grit, Mann-Whitney *U*-test	P = 0.020	

The fresh weight of all food items studied was >1.8 kg, and the mean weight of food per crop was similar between sexes (Table 2). The Mann-Whitney *U*-test was also used to evaluate possible sex-related differences in mean weight (per crop) of some types of food. The Wilcoxon matched-pairs test was used for the intra-sexual comparisons of the mean weight of food types or fodder groups.

After a list of types of food was obtained, the abundance of food plants in the field was inventoried in May and June of 2004 and in May of 2006. Only field-layer plants that had been recorded in crops were included (dwarf shrubs, herbs, grasses and sedges). The abundance of each plant species was estimated visually format 190 points situated along survey transects (415 km) on the following scale: many (2) – few (1) – absent (0). Points were established at random along the transects, and were stratified to ensure adequate coverage of the entire area. Each species (or a group of species) was assigned to one of the four habitat-association groups: (1) forest plants (habitat with close canopy; n = 43 estimates); (2) forest-edge plants (open forests, all forest edges, burns, clear-cuts; n = 50); (3) bog plants (n = 45); and (4) track-side plants (n = 52).

Attribution of plant species to one of the four habitat-association groups was straightforward, except for horsetails (*Equisetum sylvaticum*, *E. hyemale*, *E. fluviatile*), geranium (*Geranium sylvaticum*) and small reeds (*Calamagrostis epigejos*, *C.* spp.). Their final attribution to groups was done by consulting a botanist at the Pinega Reserve (see Acknowledgements). The small reeds were abundant both in clear-cuts and along tracks. However, they were attributed to the track-side group because in clear-cuts they were most abundant adjacent to tracks, and in May at these track-side sites the plants were at a more advanced development phase, i.e., they had taller stems or better visible reproductive organs. The geranium was attributed to the track-side group for the same reason, with maximal development in May. Barley (*Hordeum vulgare*) was recorded in one crop and was also attributed to the track-side group, because there were no cereal fields in the study area, and birds could therefore probably only find barley along tracks.

3. Results

3.1. General aspects of Capercaillie spring diet

Most Capercaillie food items were remains of tree- or shrub-layer plants, from the groups of forest-edge and bog plants, and especially from the group of track-side plants; forest plants were less often recorded (Table 3). Spruce seeds were found in hen but not in cock crops. In each crop containing such seeds, also sand was found. Females may have eaten spruce seeds on forest tracks in sites sheltered from the wind, where spruce seeds had also accumulated in considerable numbers (author's pers. obs.). Such accumulations of seeds could facilitate their use by Capercaillie and increase the attractiveness of this food. Spruce seeds were attributed to track-side foods.

Although *Equisetum hyemale* was not attributed to the track-side group, it was also abundant along tracks, as were flowering specimens of willow (*Salix caprea*, *S. phyllicifolia*, *S.* spp.). *Equisetum fluviatile* was common on track-side bogs formed by track embankments blocking brooks. These foods were probably also frequently eaten along tracks by Capercaillie.

The total weights of mosses (stems of *Dicranum* spp., *Pleurosium* spp., *Hylocomium* spp., stems and sporiferous organs of *Polytrichum* spp.) and lichens (*Peltigera spuria*, *P.* spp., *Usnea* spp.) in the Capercaillie diet were low (< 1%). Arthropods were also occasionally found, but the total weight of animals in the diet of both sexes was lo-

Table 3. Proportions (mean%, fresh weight) of higher plants in May diet of Capercaillie from the Pinega district of the Arkhangelsk region (1999–2006); "+" indicates <0.1%. Values in parentheses show mean weight per crop±SD in g of the most common food items. Differences in proportions between sexes: * = *P* <0.05 and ** = *P* <0.01.

Food item	Plant parts	Males (*n* = 40)	Females (*n* = 23)
Plants of tree and shrub layers, total	–	45.4 (13.3±21.8)	18.5 (5.1±19.1)**
Larix sibirica	needles, pollen cones, stems	26.9 (7.9±22.1)	15.6 (4.3±19.2)
Pinus sylvestris	needles, cones, stems	15.1 (4.4±7.5)	2.1 (0.6±1.6)**
Betula pubescens, *B. pendula*, *B.* sp.	buds, leaves, stems	2.4 (0.7±2.8)	+
Rosa acicularis, *R. majalis*, *R.* sp.	buds, leaves, stems	0.4	+
Juniperus communis, *J. sibirica*	needles, stems	0.3	+
Sorbus aucuparia	buds, leaves	0.2	0
Betula nana, *B. nana* × *B. humilis*	catkins, buds, leaves, stems	+	0.4
Salix caprea, *S.* sp.	flower buts, leaves	+	0.3
Picea obovata, P. obovata × *P. abies*	needles, cones, stems	+	+
Populus tremula	flower buds, leaves	+	0
Forest field-layer plants, total	–	10.9 (3.2±9.3)	0.6 (0.2±0.4)
Vaccinium myrtillus	buds, leaves, stems	10.8 (3.2±9.3)	0.5*
Equisetum sylvaticum	green stems	+	+
Luzula sp.	seeds, leaves	+	+
Oxalis acetosella	leaves	0	+
Forest-edge field-layer plants, total	–	11.1 (3.3±16.8)	13.3 (3.7±5.8)**
Vaccinium vitis-idaea	berries	10.3 (3.0±16.8)	0
Vaccinium uliginosum	buds, stems, leaves, berries	0.5	0
Vaccinium vitis-idaea	flower buds, leaves, stems	0.2	1.1 (0.3±1.4)
Orobus vernus	leaves, stems, buds, flowers	+	5.9 (1.6±3.5)**
Calluna vulgaris	leaves, stems, flowers	+	+
Empetrum nigrum, *E. hermaphroditum*	stems, leaves	+	+
Melampyrum cristatum, *M. pratense*, *M.* sp.	leaves, stems, seeds	+	+
Equisetum hyemale	green stems	0	1.4 (0.4±1.8)
Cerastium holosteoides, *C.* sp.	leaves, stems	0	+
Pulstatilla patens	flower, buds	0	4.8 (1.3±4.6)
Bog field-layer plants, total	–	29.4 (8.6±24.3)	39.6 (10.9±32.7)
Eriophorum vaginatum	buds	17.3 (5.1±19.6)	3.6 (1.0±4.7)
Oxycoccus sp.	berries, leaves, stems	10.5 (3.1±12.0)	23.4 (6.4±20.3)
Andromeda polifolia	buds, leaves, stems	1.5 (0.4±1.2)	10.8 (3.0±8.6)
Chamaedaphne calyculata	leaves	+	+
Equisetum fluviatile	green stems	0	1.8 (0.5±1.7)
Carex leporina, *C.* sp.	seeds, leaves	0	+
Track-side field-layer plants, total	–	2.6 (0.8±4.7)	27.8 (7.7±12.4)**
Tussilago farfara	buts, flowers, stems	2.5 (0.7±4.7)	19.1 (5.3±12.4)**
Leontodon autumnalis	leave shoots	0.1	0
Hordeum vulgare	grain	+	0
Poaceae	leaf shoots	+	0
Filipendula ulmaria	leaf shoots	+	0
Picea obovata, P. obovata × *P. abies*	seeds	0	5.1 (1.4±3.6)
Trifolium hybridum, *T. repens*, *T.* sp.	leaf shoots	0	2.5 (0.7±3.1)
Calamagrostis epigejos, C. sp.	leaf shoots	0	0.3
Veronica longifolia, *V.* sp.	leaf shoots	0	0.3
Ranunculus acris, *R. repens*, *R.* sp.	leaf shoots	0	0.2
Geranium sylvaticum, *G. Pratense*, *G.* sp.	leaf shoots	0	0.2
Chamaenerion angustifolium	leaf shoots	0	+
Carex limosa	seeds, leaves	0	+
Polygala amarelle	leaf shoots	0	+
Achillea millefolium	leaves	0	+
Cirsium heterophyllum, *C.* sp.	leaf shoots	0	+
Herbs, undetermined	leaves	0	+

Table 4. Intra-sexual differences (*P* values from Wilcoxon matched-pairs test) between mean fresh weight (per crop) of the principal fodder groups in the diet of Capercaillie from Pinega district during 1999–2006. Column abbreviations for field-layer plant groups: Forest = forest-interior plants; Edge = forest-edge plants; Bog = bog-associated plants; Track = track-side plants; Tree-shrub = tree- and shrub-layer plants.

Group	Males				Females			
	Forest	Edge	Bog	Track	Forest	Edge	Bog	Track
Tree-shrub	<0.001	<0.001	0.014	<0.001	0.006	0.339	0.936	0.079
Forest	–	0.520	0.411	0.009	–	0.004	0.069	<0.001
Edge	–	–	0.171	0.117	–	–	0.381	0.163
Bog	–	–	–	0.014	–	–	–	0.243

wer than 1%. In females, only imagines of *Formica rufa* and *F.* spp. were recorded. Animal foods of males were more variable: imagines of *Lochmaeae caprea*, *Plateumaris sericea*, *Altica* spp., larvae of *Ellopia fasciaria*, pupae, and imagines of *Formica rufa* and *F.* spp.

3.2. Diets of cocks and hens

Food items of the tree- and shrub-layer plants dominated the diet of cocks, making up ca. 45% of the food eaten, followed by bog plants with ca. 29% (Table 3). Proportions of forest-edge and forest plants were ca. 11% each. Trackside plants were of minor importance in the male diet (<3%). Mean weight per crop of the tree and shrub foods was significantly higher than that of any other fodder group (Table 4), and that of the track-side plants lower than all but the forest-edge group.

Although the study area was heavily managed, with extensive clear-cuts, plants of the native habitats formed the main part of the cock diet (96.7%). These comprised all tree and shrub foods (except spruce seeds), ericaceous dwarf shrubs and cottongrass (*Eriophorum vaginatum*). The mean weight per crop of all these plants was significantly higher than that of all other higher plants (28.4 ± 45.8 g *vs.* 0.8 ± 4.8 g; P <0.001).

In male diet, fragments of pine and larch were the main types of food from the tree and shrub layers (Table 3). The mean weight of larch fragments (comprising the typical spring foods of Capercaillie, viz. young needles and male pollen cones) was almost twice as high as that of pine fragments (P = 0.005). Apparently the presence of larch in this region allowed cocks to gather most of their spring food on tree crowns.

In the female diet, bog plants were the most abundant fodder group (ca. 40%), followed by track-side species (ca. 28%), trees and shrubs (ca. 18%), forest-edge plants (ca. 13%), and forest plants (<1%) (Table 3). The only significant differences in the mean weight per crop were between the group of forest plants and all but the bog group of plants, which suggests a larger diversity of the hen diet compared to the cock diet.

Hens had more plants of native habitats (57.9%) than other higher plants (41.9%) in their diet, but the mean weights of these groups (16.0 ± 36.6 g *vs.* 11.5 ± 14.6 g, respectively) did not significantly differ from each other.

The track-side plants were represented by 13 components in the female diet (Table 3), but the proportion of each component was low except for coltsfoot (*Tussilago farfara*), pine seeds, and clover (*Trifolium*). The abundance of coltsfoot buds and flowers in female crops was roughly comparable with the abundance of such traditional spring foods of Capercaillie (in NW Russia) as berries of cranberry (*Oxycoccus* sp.) and buds of cottongrass. However, cranberry did not significantly differ from cottongrass or from coltsfoot, and cottongrass did not significantly differ from coltsfoot.

Coltsfoot was a common and sometimes very abundant species of the track-side habitats in the study area. In some years (especially in 1999, 2001 and 2006), I repeatedly observed long segments of tracks (200–300 m) along which every single bud and flower of coltsfoot had been snipped off by grouse. The footprints of birds on the clay adjacent to foraged plants suggested that other grouse of the study area (*Tetrao tetrix*, *Lagopus lagopus*, and *Bonasa bonasia*) also ate this plant.

3.3. Differences between sexes

The consumption of different food groups significantly differed between sexes for the tree and shrub food items (cocks had eaten almost twice as much of these as hens had; P <0.001), for the forest-edge plants (P = 0.003), and for the track-side species (which differed by roughly an order of magnitude; P <0.001). Females ate spring foods typical for Capercaillie in the study region, such as shoots of herbaceous plants, in larger amounts than males did (P <0.001). The intake of other spring foods, i.e., buds and flowers, was marginally different between males and females (P = 0.064) and not significant for over-wintered berries (P = 0.332).

Weights of typical winter foods (needles of pine, spruce, and juniper together) were lower than all other items combined in both male and female diets (P = 0.005 and P < 0.001, respectively). However, these food items were more abundant in the crops of cocks than in those of hens in terms of proportion (15.3 ± 20.3% *vs.* 2.2 ± 4.1%; P = 0.006) and weight (4.5 ± 7.4 g *vs.* 0.6 ± 1.8 g; P = 0.002).

The proportion of the forest fodder group in the diet was equally low for both sexes, and also the intake of this group was similar (P = 0.221). However, the mean weight of green fragments of bilberry in the crops of cocks was 20 times greater than in those of hens (P = 0.043).

Food plants of native habitats were significantly more abundant in the diet of cocks than in that of hens (97.6% vs. 57.9%; P = 0.001), suggesting that hens had more opportunistic feeding habits than cocks in the study area.

4. Discussion

The earlier dietary shift of Capercaillie hens, compared with cocks, from winter to spring foods is known from at least the 19th century (e.g., Sabaneev 1875) and has been confirmed by quantitative studies (Borchtchevski & Dronseyko 1989, Pulliainen & Tunkkari 1991, Storch *et al.* 1991, Borchtchevski 1995, Odden *et al.* 2003). The data in the present paper are consistent with previous conclusions: the typical winter food items were seven times greater in the spring diet of cocks as compared with hens. Also, the proportion of pine fragments in the diet of Pinega cocks may have been underestimated, as most of the cocks had been shot during daylight hours. Borchtchevski (1994a) showed that, in spring, Capercaillie show more (cocks) or less (hens) pronounced two peaks of food intake, and that the proportion of pine fragments in the male diet is 2–3 times higher during "night" (when cocks are at or nearby leks) as compared with the "daytime" hours (7–14 hours). It is also likely that the unusually early growth of larch, e.g., in 2006 allowed cocks to eat green fragments of larch instead of pine needles without otherwise altering their usual behaviour.

The complicated behaviour of cocks (Eliassen & Wegge 2007) was considered as the essential factor determining sexual differences in the dietary shift of Capercaillie in spring (Odden *et al.* 2003). However, in phytophagous (folivorous, herbivorous) animals, gut capacity increases linearly with body mass, whereas mass-specific nutritional requirements increase with decreasing body mass (Demment & Van Soest 1985). For this reason, smaller birds cannot compensate for the low quality of a food by eating more of it (Sedinger 1997). The gut of a Capercaillie male is about 25% longer than that of a female (Borchtchevski 1987). It appears to be just this difference that seems to permit the bigger males to perform their normal reproductive functions, including complex behaviour, while continuing to eat mostly poor-quality winter foods. But this is impossible for the smaller females. During snowmelt, Capercaillie hens can achieve adequate nutrition both for the laying of highly quality eggs (see Introduction) and for the accumulation of energetic resources for incubation (Borchtchevski 1993). At the same time, the observed spring decrease of body mass may be desirable for Capercaillie cocks because it facilitates their summer moult (Hissa *et al.* 1990).

A previous study on Capercaillie diet in a highly perturbed area, from the boundary of nemoral and boreal (i.e., taiga) forest, showed that a considerable part of the spring diet of both sexes, but especially cocks, comprised plants of the native taiga biotopes (Borchtchevski & Dronseyko 1989). The present paper partly confirms this conclusion with data from northern taiga: even in a highly perturbed (logged) area, such plants made up almost all the diet of cocks (ca. 97%). Females demonstrated a more opportunistic feeding strategy: hence, with regards to their spring feeding, hens may be considered as being less vulnerable to logging than males in the taiga area.

Bedrock, via soil fertility, could affect the quality of the diet of hens that are about to lay their eggs: in areas with base-richer bedrocks, the vegetation varies more and the plants may be richer in nutrients (Watson & Moss 2008). A comparison of the present data with other North European studies suggests that soil fertility determines the species richness and diversity of vegetation, which in turn allows Capercaillie to eat a wider range of foods. So, the Pinega district lies on base-rich limestones and dolomites with fertile, carbonated soils and diverse vegetation. Here, approx. 15% of the female diet comprised of young needles and pollen cones of larch (Table 3). This plant species avoids infertile, acidic soils and is not known to belong to Capercaillie diet in the base-poor granite and gneiss areas of the Fennoscandian shield (Neifel'd 1958, Semenov-Tian-Shansky 1960, Seiskari 1962, Pulliainen 1970, Ivanter 1974, Pulliainen & Tunkkari 1991, Borchtchevski 1994b, Annenkov 1995, Kashevarov & Pozdnyakov 1997, Odden *et al.* 2003). Soil fertility and vegetation richness also allow Capercaillie cocks to have a more varying diet. The presence of larch in the Pinega area allows cocks to forage for their typical spring foods on tree crowns rather than on the ground, which is considered to be optimal feeding behaviour for Capercaillie males in spring (Odden *et al.* 2003).

This study revealed significant sex-dependent differences in the consumption of track-side plants; these were more eaten by hens but not by cocks. Also, along tracks, the hens ate some plants of the other trophotopes and also spruce seeds. Considering these food items, track-side plants might comprise a third of the hen diet. Spruce seeds may not be typical food for Capercaillie, although their consumption has previously been reported in the Ukraine Carpathians (Ostrovskiy 1974) and in Byelorussia (T. Pavlushchik, pers. comm.).

Grit is common on track-side patches but was not abundant in the crops of Pinega Capercaillie (Table 2). Sand was recorded among the feathers and skins of only 9% of cocks and 20% of hens. However, one cannot judge the frequency of Capercaillie sand-bathing from these numbers, because it is not known how long sand remains in the feathers of birds. Nonetheless, feeding was apparently the major reason why Capercaillie (especially hens) used track-side patches. In any case, the high proportion of track-side plants in the diet of females obliges one to consider forest tracks as an important spring trophotope. Therefore, a complete elimination of forest tracks may not be a good technique for Capercaillie management in north-western Russia. However, it should not be applied to western European populations of Capercaillie either.

Some analyses of crop contents and gizzards apply to cocks, hunted on leks, but not to females (e.g., Almăşan 1970, Kohl 1972, Lindner 1977, De Franceshi 1994). Faecal analyses have shown that spring diets of Capercaillie are composed mostly of fragments of arbuscular species, such as beech (*Fagus sylvatica*) and Scots pine (e.g., Chapuis *et al.* 1986, Heinemann 1989, Storch *et al.* 1991, Picozzi *et al.* 1996, Rodrígues & Obeso 2000, Summers *et al.* 2004). Hence, Capercaillie appear to only little depend on the availability of ground foods, and the elimination of forest tracks would only marginally affect their food resources. On the other hand, owing to methodological difficulties, faecal analyses reveal mostly coarse foods (fragments of arbuscular plants, stems of bilberry etc.), whereas easily digestible items are underestimated (Picozzi *et al.* 1999, Rodrígues & Obeso 2000). Simultaneously, in spring, it is just the easiest-digestible parts of field-layer plants: young shoots, flower buds, and flowers, that are most attractive for laying hens (Semenov-Tian-Shansky 1960, Borchtchevski 1995, this paper). Earlier Rodríguez and Obeso (2000) have reported the low fodder value of beech, due to the high fiber content of its buds and low density of food items on beech branches compared to pine. But faecal analysis could also underestimate the intake of easily-digestible food items gathered from arbuscular plants, such as beech flower buds and flowers, which are attractive for hens (Leclercq 1987). Moreover, coltsfoot has previously been recorded in the diet of West-European Capercaillie only in a study based on visual observations (Saniga 1998), but has not been reported in other "western" publications.

Strong evidence of a negative influence of tracks on Capercaillie populations has also been reported from Finland. There, a decline in the proportion of females was recorded in the Capercaillie population from 1964–88 (Helle *et al.* 2000). The authors suggested that the behaviour of hens – that often visit roads in spring – was one of the most likely causes of the decline, due to increasing traffic mortality or predation at or near roads. The Pinega data show that females gather about ten times as much food along tracks as do males, and hence spend considerably more time there. A paper on predation near tracks showed an attractiveness of tracks for some raptors (Meunier *et al.* 2001). Also, in the forests of the Russian Plain, the remains of birds, killed by predators, were more frequent on or near forest tracks and forestry cut-lines than in forest interiors (V. Borchtchevski & A. Kostin, unpubl. data). Hence, tracks are both a source of disturbance and sites of higher predation risk. But should they be eliminated?

The adaptation of Capercaillie to eat track-side pioneer plants was probably acquired during ancient epochs, when all vegetative complexes were influenced by large phytophagous mammals, the numbers of which were not yet catastrophically reduced by man. According to a reconstruction of the last Pleistocene epoch in Eastern Europe, the vast area between the White and Black Seas was occupied by a climax stage of very sparse tree vegetation, maintained by the heavy grazing and trampling of large mammals (Kaliyakin 2004); the soil was disturbed and pioneer forbs and grasses dominated the field layer, a zoogenic forest-steppe. It is important to emphasize that there were numerous albeit scattered patches of bare ground that were often trampled down by mammals.

Hence, most of the Russian Plain (and perhaps all of Eurasia) was characterized by areas similar to contemporary patches of trackside microcoenoses. In spring, this situation provided extensive access for Capercaillie to pioneering ground vegetation and reduced the amount of time spent foraging for sparse plants, thereby decreasing predation risk.

Present tracks across forest patches force Capercaillie hens to aggregate to narrow strips that are habitat prone for predation. But if food for hens were super-abundant on such sites, foraging time would decrease and predator avoidance might become easier. Based on this chain of thought one might propose the following principles of track reorganization for Capercaillie management.

The managers should close a track segment from cars and hikers, and plough it up in order to create (1) a fire barrier and (2) a site for the development of weedy herbaceous vegetation. There, the sowing of plants providing many shoots in early spring would increase the density of food items and consequently decrease the time spent by hens in search for food. It is important to stress that such spring food should be abundant throughout the managed area, so that the appearance of hens at any given site would be unpredictable for a predator. The species of plant to be sowed would depend on geographical position. Coltsfoot may be a good prospect in northeastern Europe. The occupation by this weed plant of forest coenoses adjacent to tracks is usually low, however, probably because it is a pioneer species. The addition of coltsfoot along with other species with similar attractiveness for hens (though differing slightly in flowering phenology; e.g., *Pulstatilla patens*, *Ficaria verna*, *Primula vernis*, *Anemone sylvestris*, *A. ranunculoides*, *A. nemorosum*, *Pulmonaria obscura*) may provide food for hens during both egg-laying and incubating periods, with low sensitivity of the food source to large inter-annual fluctuations in shoot abundance. Hens of other grouse species may also use such “track-flower-beds” (as true Ladies).

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Metson (*Tetrao urogallus*) toukokuinen ruokavalio laajalti hakatulla alueella Luoteis-Venäjällä

Metson kuvun sisältöä toukokuussa tutkittiin ensi kertaa Luoteis-Venäjällä alueella, jolla metsätalous on intensiivistä. Puu- ja pensaskerros sekä suokasvit muodostivat sekä kukkojen että koppe-

loiden ravinnon pääosan (vastaavasti 75 % ja 58 % kuvun sisältämän ravinnon tuorepainosta). Männyn ja mustikan jäänteet olivat yleisempiä kukkojen kuvuissa, kun koppelot olivat käyttäneet ravinnokseen enemmän ruoho- ja tienvarsikasveja. Koppelot myös söivät teiden varsilta kuusten siemeniä. Tienvarsien tarjoamat ravintokohteet muodostivat jopa kolmanneksen koppeloiden ravinnosta. Nämä sisälsivät apiloiden versoja sekä erityisesti leskenlehden kukintoja.

Metsäteiden kertakaikkinen, laajamittainen poisto metsokantojen hoitokeinona saattaisi siten vähentää koppeloille tärkeitä ruokailualueita valtaosassa lajin Itä-Euroopan levinneisyysaluetta. Teiden sulkeminen ihmiskäytöstä sekä niiden muuttaminen runsaasti keväällä kukkivia kasveja käsittäviksi kohteiksi saattaa olla koppeloiden kannalta parempi vaihtoehto. Jopa tutkitun kaltaisella, laajalti hakatulla alueella metsokukkojen ravinto koostui pääosin (97 %) taigan kotoperäisestä kasvilajistosta. Kukkoihin verrattuna koppeloiden ravinnonkäyttö oli siis opportunistisempaa; siten hakkuut saattavat enemmän uhata kukkojen ravinnonsaantia.

References

Almăşan, H.A. 1970. Beitrag zur kenntnis der narhung des auerhahns (*Tetrao urogallus* L.) während der balzzeit. — Zeitschrift für Jagdwissenschaft, 16: 7–13. [In German.]

Annenkov, V.G. 1995. Grouse of Karelia (biology, population dynamic, perspectives of use). — These, Institute of Biology, Petrozavodsk. [In Russian.]

Borchtchevski, V.G. 1986. On the vegetative foods of capercaillie. — The questions of hunting ornithology (ed. Gusakov, E.S.): 109–128. Moscow. [In Russian.]

Borchtchevski, V.G. 1987. On the gut size of common capercaillie. — Rearing of the valuable and rare animals (ed. Gabuzov, O.S.): 61–68. Moscow. [In Russian.]

Borchtchevski, V.G. 1993. Population biology of capercaillie. Principles of the structural organization. — Ed. of Central Laboratory of Game Management. Moscow. [In Russian.]

Borchtchevski, V.G. 1994a. Alimentation journalière du grand tétras (*Tetrao urogallus*) au printemps dans l'ouest de la taïga russe. — Gibier Faune Sauvage, Game and Wildlife 11: 219–233. [In French.]

Borchtchevski, V.G. 1994b. Régime alimentaire des juvéniles et des adultes grands tétras (*Tetrao urogallus*) dans l'ouest de la taïga russe — Gibier Faune Sauvage, Game and Wildlife, 11: 21–38. [In French.]

Borchtchevski, V.G. 1995. Comparaison des régimes alimentaires printaniers des mâles et des femelles de grand tétras (*Tetrao urogallus*) dans la taïga russe. — Gibier Faune Sauvage, Game and Wildlife 12: 303–320. [In French.]

Borchtchevski, V.G. & Dronseyko, E.G. 1989. Feeding of capercaillie in north of the Ivanovo region. — The grouses in reserves of RSFSR (ed. Ivanter, E.V.): 73–80. Moscow. [In Russian.]

Borchtchevski, V.G., Wegge, P. & Hjeljord, O. 2006. The dependent and not dependent of density reproductive success in sympatric grouse populations. — News of the Game Management 3 (3): 278–288. [In Russian.]

Chapuis, J.L., Bernard-Laurent, A., Didilon, M.C., Jacob, L. & Ponce, F. 1986. Régime alimentaire des Galliformes de montagne. Synthèse bibliographique et méthodes d'etudes. — Museum National d'Histoire Naturelle, Minister de l'Environnement. Paris. [In French.]

De Franceschi, P.F. 1994. Status, geographical distribution and limiting factors of capercaillie (*Tetrao urogallus*) in Italy. — Gibier Faune Sauvage, Game and Wildlife 11 (special issue, part 2): 161–183.

Demment, M.W. & Van Soest, P.J. 1985. A nutritional explanation for body size patterns of ruminant and nonruminant herbivores. — American Naturalist, 125: 641–672.

Eliassen, S., & Wegge, P. 2007. Ranging behaviour of males capercaillie *Terao urogallus* outside lekking ground in spring. — Journal of Avian Biology 38: 37–43.

Heinemann, U. 1989. Zur winternahrung des auerhuhns (*Tetrao urogallus* L.) im Harz (Niedersachsen). — Zeitschrift für Jagdwissenschaft 35: 35–40. [In German]

Helle P., Lindén, H., Kurki, S., Rätti, O. & Kumpu, P. 2000. Suomen metsokannan sukupuolten lukusuhde muuttunut. — Suomen Riista 46: 14–26. [In Finnish.]

Hissa, R., Rintamäki, H., Virtanen, P., Lindén H. & Vihko, V. 1990. Metson energiavarastot. — Suomen Riista 6: 62–71. [In Finnish.]

Ivanter, E.V. 1974. Capercaillie and willow grouse in Karelia. — Ornithology (Moscow) 2: 206–226. [In Russian.]

Kashevarov, B.N. & Pozdnyakov, S.A. 1997. Tetraonidae of the Kostomusha Nature Reserve. — Ecosystems, fauna and flora of the Finnish-Russia Reserve Friendship (eds. Lindholm, T., Heikkilä, R. & Heikkilä, M.) : 187–193. Helsinki, Finnish Environment Institute.

Kaliyakin, V.N. 2004. The nature conditions of late Pleistocene. — Eastern-European forests: the history in Holocene and contemporaneity. (ed. Smirnova, O.V.): 59–92. Moscow, Nauka. [In Russian].

Kohl, Ş. 1972. Angaben zur ernährung des auerhahnes (*Tetrao urogallus* L.) während der balzzeit. — Ochrana Fauny (Bratislava) 6: 98–104. [In German.]

Lindner, A. 1977. Das auerhuhn. — Die Waldhuhner (ed. Parey, P.): 11–64. Hamburg & Berlin. [In German]

Leclercq, B. 1987. Ecologie et dynamiques des populations du grand tétras (*Tetrao urogallus major* L.) dans le Jura Français. — Thèse de l'Univer. de Bourgogne, Dijon. [In French.]

Lobashchev, S.V. & Shcherbakov, F.A. 1936. Natural foods of capercaillie in yearling cycle of life and in summer brood stations in connection with problems of hunting management. — Zoological Journal (Moscow) 15: 307–320. [In Russian.]

Meunier, F., Fichet, X. & Verheyden, Ch. 2001. Utilisation des empris autoroutierès par les rapaces diurnes à différentes échelles spatiales et temporelles. — Alauda 69 (1): 117–127. [In French.]

Neifel'd, I. A. 1958. The fending of some forest birds of southern Karelia. — Zoological Journal (Moscow) 37 (2): 257–269. [In Russian]

Odden, M., Wegge, P., Eliassen, S. & Fine, M.H. 2003. The influence of sexual dimorphism on the dietary shift of capercaillie *Tetrao urogallus* during spring. — Ornis Fennica 80: 130–136.

Ostrovskiy, A.I. 1974. Some particularities of Carpathian population of capercaillie. — In Transactions of the 6th All-Soviet Union Ornithological Conference: 96–97. Moscow, part 2. [In Russian.]

Pulliainen, E. 1979. Autumn and winter nutrition of the capercaillie (*Tetrao urogallus*) in the northern Finnish taiga. — In Woodland Grouse (ed. Lovel, T.P.I.): 92–97. World Pheasant Assoc., Bures, Suffolk.

Pulliainen, E. & Tunkkari, P.S. 1991. Response by capercaillie *Tetrao urogallus* and the willow grouse *Lagopus lagopus*, to the green matter available in early spring. — Holarctic Ecology 14: 156–160.

Picozzi, N., Moss, R., & Catt, D.C. 1996. Capercaillie habitat, diet and management in a Sitka spruce plantation in central Scotland. — Forestry 69: 373–388.

Picozzi, N., Moss, R. & Kortland, K. 1999. Diet and survival of capercaillie *Tetrao urogallus* chicks in Scotland. — Wildlife Biology 5: 11–23.

Rodríguez, A.E., & Obeso, J.R. 2000. Diet of the Cantabrian capercaillie: geographic variation and energetic content. — Ardeola 47: 77–83.

Sabaneev, L.P. 1875. Capercaillie. Hunting monograph. — Nature. Nature and Historical Collection (Moscow) 3: 1–58. [In Russian.]

Saniga, M. 1998. Diet of capercaillie (*Tetrao urogallus*) in Central-European mixed spruce-beech-fir and mountain spruce forest. — Folia Zoologica 47: 115–124.

Scherzinger, W. 2003. Arttenschutyproject Auerhuhn im Nationalpark Bayerisscher Wald von 1985–2000. — Nationalpark Bayerisscher Wald. Grafenau. [In German.].

Sedinger, J.S. 1997. Adaptation to and consequences of an herbivorous diet in grouse and waterfowl. — Condor 99: 314–326.

Seiskari, P. 1962. On the winter ecology of the capercaillie, *Tetrao urogallus*, and black grouse, *Lyrurus tetrix*, in Finland. — Paper Game Research, 22: 1–119.

Semenov-Tian-Shansky, O.I. 1960. On ecology of Tetraonids. — Transactions of the Lapland State Reserve (Moscow) 5: 5–319. [In Russian.]

Sleptsov, M.M. 1948. The method of study of the intensity of the bird reproduction by the ovaries. — Protection of Nature (Moscow) 5: 119–129. [In Russian]

Summers, R.W., Proctor, R., Thorton, M., & Avey, G. 2004. Habitat selection and diet of the capercaillie *Tetrao urogallus* in Abernethy Forest, Strathspey, Scotland. — Bird Study 51: 58–68.

Summers, R.W., McFarlane, J. & Perce-Higgis, J.W. 2007. Measuring avoidance by capercaillie *Tetrao urogallus* of woodland close to tracks. — Wildlife Biology 13: 19–27.

Storch, I., Schwarzmüller, Ch. & von den Stemmen, D. 1991. The diet of capercaillie in the Alps: a comparison of hens and cocks. — Transactions of the 20th IUGB-Congress: 630–635. Godollo (Hungary).

Storch, I. 2000. Grouse. Status, survey and conservation action plan 2000–2004. — World Pheasant Association, BirdLife, SSC Grouse Specialist Group.

Teplov, V.P. 1947. Capercaillie in the Petchora-Ilich reserve. — Transactions of the Petcora-Ilich Reserve (Moscow) 4 (1): 3–76. [In Russian.]

Thiel, D., Ménoni, E., Brenot, J.-C., & Jenni, L. 2007. Effects of recreation and hunting on flushing distance of capercaillie. — Journal of Wildlife Management 71: 1784–1792.

Watson, A. & Moss, R. 2008. Grouse. The natural history of British and Irish species. — (Collins ed.) London.

Appendix. Data collecting for the present study.

Capercaillie is a common game species in most parts of the Russian Federation, although it is protected in many administrative regions adjacent to the southern boundary of the boreal forest zone (e.g., Kaluga, Penza, Republic of Bashkiria, etc.). During several years of the present study, restricted spring hunting of Capercaillie males at leks by aboriginal hunters was officially authorized in the Arkhangelsk region. The data on 27 males shot this way were thus initially collected by aboriginal hunters, and the author took the advantage of this legal hunting that would have taken place independent of the present study.

This hunting is controlled by the Arkhangelsk Regional Office of Game Management that can ban hunting in any season or district. Additional three males and three females were found dead (i.e, had not been shot). Moreover, 10 males and 20 females were hunted under special authorizations granted by the State Service of Game Management, a government institute that can grant authorizations for shooting game animals off the hunting season for scientific purposes.

In the present study, the authorizations were obtained following the instructions and protocols of the State Centre of Game Management under its permanent research program systems of rational use of the grouse resources in Russian Federation. This program aims at investigating large-scale variation of Arkhangelsk Capercaillie subpopulations of the native taiga forests (Onega district; Borchtchevski 1993, Borchtchevski & Moss in litt.), and from the logged and native forests of Pinega and Mezen districts (the present study).

Apart from data on Capercaillie diet, presented here, data on age composition (by cranial analysis), breeding phenology and reproductive potential (by hen ovaries), parasitic invasions (by intestines), morphometry, fat reserves and traumatism (by bird carcasses) were collected from the shot individuals (to be published in forthcoming papers).