Ornis Fennica 91:14–28. 2014

Age structure of Capercaillie males (*Tetrao urogallus*) in NW Russia may reflect two-way movements – a hypothesis

Vladimir Borchtchevski* & Robert Moss

*V. Borchtchevski, I.K. Skryabin' State Academy of Veterinary Science, Medicine & Biotechnology, Moscow, Russia. * Corresponding author's e-mail: megra@mail.ru*
R. Moss, Station House, Crathes, Banchory, Kincardineshire AB31 5JN, Scotland

Received 19 October 2012, accepted 23 June 2013

Skulls of Capercaillie (*Tetrao urogallus*) males collected in NW Russia in 1980–2008 showed two different types of age structure. In native forest and bog-forest tracts with high Capercaillie density (~ 2.0 birds / km^2 in spring) there were relatively more 2- and 3-year-old males and correspondingly fewer yearlings and youngsters. The converse applied over the vast adjacent logged areas where Capercaillie density was lower (~ 0.6 birds / km^2), with fewer 2- and 3-year-old males and more yearlings and youngsters. The results were consistent with emigration of youngsters from native into logged areas and a reverse movement of maturing cocks attempting to join the big leks on native areas. The evidence suggested that survival of cocks over 3 years old was low in both habitat types, perhaps due to continued emigration from logged areas plus mortality associated with competition for status at the big leks on native areas. Such movements presumably occur mostly at times of high population density.

1. Introduction

The Capercaillie (*Tetrao urogallus*) is a big, polygamous grouse whose usual habitat is old coniferous forest. In spring, cocks display together at traditional sites called leks, where adult males are territorial (Wegge & Larsen 1987). Many authorities consider Capercaillie to be a mostly sedentary species (Semenov-Tian-Shansky 1960, Romanov 1979, Potapov 1985). If so, recruitment to a population by immigrants must be negligible, and the average age structure over a sufficiently long series of years must be pyramidal, with successively fewer birds in each older age cohort. Below, such age distributions are called "balanced".

Even in sedentary populations, however, "unbalanced" distributions with more birds in some older cohorts can occur over short runs of years. This happens in cyclic or fluctuating populations because recruitment of the youngest cohort is low during periods of population decline and high during periods of population growth. There are examples of this from Finland (Lindén 1988, 1989, Lindström *et al*. 1997) and Central Russia (Dronseiko & Nemnonov 1984). However, unbalanced age distributions have been recorded from a non-cyclic population in which spring density varied little from year to year (Borchtchevski 1993), and from a cyclic population representatively sampled at all stages of the population cycle (Borchtchevski & Sivkov 2010). The authors explain such unbalanced distributions by long-distance movements of birds.

Indeed, Capercaillie in some regions migrate tens of km between their seasonal ranges (Kirikov 1952, Kuzmina 1968). This might be seen as an

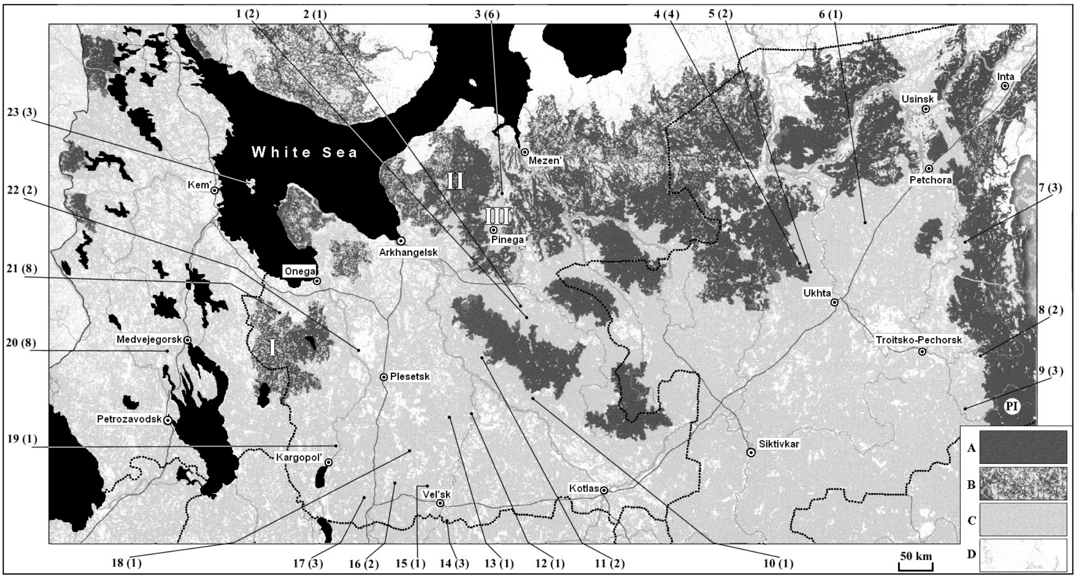

Fig. 1. Vegetation (according to Aksenov *et al.* 2002): A – native forest, B – native bog-forest tracts, C – logged areas, D – unforested areas) and sites of data collection in NW Russia. Bird samples were from areas: I – the Onega' tract (Borchtchevski 1993), II and III – the Belomor' tract and adjoining logged areas (for more details see Fig. 2), IV – various sites in logged forest (Borchtchevski 2011) represented by 23 points, with identifying numbers (and number of birds in parentheses) in the margins. PI – the Pechoro-Ilich Reserve.

extreme, coarse-grain variant of the "landscape mosaic" hypothesis (Rolstad & Wegge 1989), in which a low degree of habitat interspersion triggers seasonal movements (Hjeljord et al. 2000). But this does not explain the unbalanced age distributions, which were noted at all seasons (Borchtchevski 1993, Borchtchevski & Sivkov 2010).

Also, there is indirect evidence suggesting long-distance irruptive or migratory movements, some over 1,000 km (Siivonen 1952, Couturier & Couturier 1980, Cramp & Simmons 1980, Potapov 1985, Liukkonen-Anttila *et al.* 2004). Sporadically, Capercaillie individuals or flocks are seen flying nonstop at unusually high altitudes of up to 1 km, mostly in spring and autumn. In NW Russia, past records involve large flocks of Capercaillie (Potapov 1985), with smaller numbers in recent decades (Borchtchevski 1993, Borchtchevski & Sivkov 2010). But the causes of such movements remain unclear.

Another insight into unbalanced age distributions comes from the idea of spatially structured populations, such as the source-sink model (Pulliam 1988). In this, birds disperse from a source habitat into a sink. In Capercaillie, the apparent sink may act as a population reserve and provide a reverse stream of birds to the erstwhile source (Moss & Oswald 1985, Moss 1987b, Moss & Weir 1987), a pattern of movement that is neither standard source-sink nor metapopulation. To avoid preconceptions, we consider below a "two-compartment" (or "two-way") model with movement in either direction. If birds dispersing between compartments come from specific age cohorts, they can cause unbalanced age distributions in either compartment.

Such a model was proposed for a large bog-forest massif in NW Russia (Borchtchevski 1993). This involved: stream 1 (source-sink) – dispersion of mostly young birds from better to poor habitat, and stream 2 (sink-source) – movement of middle-aged individuals from poor to better habitat, so presumably increasing their fitness.

The distance of such putative movements might be 100 km or more (Borchtchevski 1993). Conceptually, this hypothesis is a two-compartment model with two-way movement. It nonetheless accommodates the real situation, in which discrete tracts of native forest (better habitat) occur within a logged landscape (poor habitat).

Below, we: 1) collate data (Borchtchevski 1993, 2011, Borchtchevski & Sivkov 2010) on the age structure of Capercaillie cocks in NW Russia; 2) show that this differs between native and logged forest; and 3) that the observed differences are consistent with the two-compartment hypothesis. We also give evidence 4) that the survival of cocks > 3 years old is unusually low in both habitats, suggesting that two-way movement is driven by competition for place or status in native forest.

2. Material and methods

2.1. Study areas

Cocks were collected in the flat taiga of NW Russia, bounded by parallels 66°04’ N and 60°46’ N and meridians 33°52’ E and 57°57’ E (total area ~ 400,000 km^2). There are two broad vegetation types: 1) unlogged forest and bog-forest tracts (“native”) and 2) complex of secondary vegetation on the sites of clear cuttings, burns and abandoned farmland (“logged”) (Figs 1, 2).

The native areas are occupied by old (> 120 years) coniferous forests (of *Picea abies, P. obovata*, *P. fennica*, *Pinus sylvestris, P. sibirica* and *Larix sibirica*) mixed with parvifoliate species (*Betula pendula, B. pubescens*, *Populus tremula*). Dwarf shrubs (Ericaceae, Vaccinaceae, Empetraceae) dominate the field layer, forbs being common on rich soils. Dwarf shrubs, sphagnum mosses (Sphagnidae) and sedges (Cyperaceae) comprise the field layer of the peat bogs that form a proportion varying from about 5% to 50% of the native area.

Dense secondary forests (mostly young) dominated by parvifoliate species form the main vegetation of logged areas. These comprise a mosaic of open and overgrown clear-cuts, bogs, networks of mostly-abandoned timber-hauling tracks, young plantations of coniferous species, and small patches of old forest (Borchtchevski 2009). Clear-cuts are characterised by varied coarse-grained mosaics of dwarf shrubs, forbs (*Epilobium* spp., *Chamaenerion angustifolium, Geranium sylvaticum* etc.), or tall shrubs (*Rubus idaeus*, *Sorbus aucuparia, Alnus incana, Salix caprea*) with a smaller proportion of grass (*Calamagrostis epigeios, C. neglecta, Deschampsia cespitosa* etc.) (for more details see Melekhov *et al*. 1965).

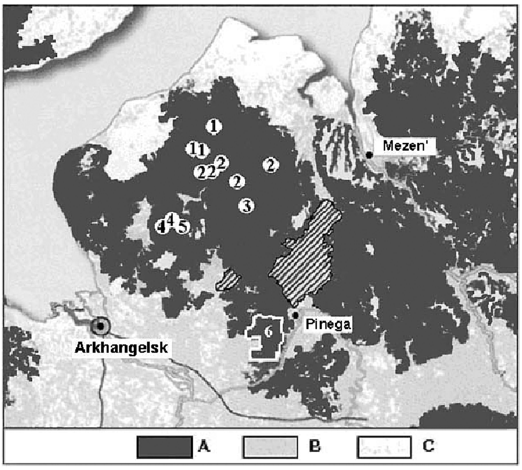

Fig. 2. Vegetation (A – native tracts, B – logged areas, C – unforested areas, for more details see Fig. 1) and disposition of sites where skulls were collected (from Borchtchevski & Sivkov 2010). The white points (1–5) and white outline (6 – the Pinega Reserve) indicate collections within native forest tracts. The hatched areas show the two main sites of collection on logged areas.

In the western logged areas (points 1, 14, 21 in Fig. 1, hatched contours in Fig. 2), spring Capercaillie density is ~ 0.6 (0.3–0.8) birds / km^2, but it is higher in the western native areas (tract I on Fig. 1, points 1 and 6 on Fig. 2): ~ 2.0 (0.8–2.8) birds / km^2 over the entire landscape and > 6 birds / km^2 on some habitat (Borchtchevski 2003, 2009; Borchtchevski & Sivkov 2009). There are no comparable spring data for eastern parts of the study area.

Regularly spaced large Capercaillie leks (from 20–40 to ≥ 100 cocks / lek) are characteristic of native areas (Borchtchevski 1993, Rolstad *et al.* 2009), whereas small infrequent leks averaging 2–3 cocks / lek typify logged areas (Borchtchevski 2011). So, in the entire region (Fig. 1), areas with low Capercaillie density adjoin tracts where density seems close to the maximum for the entire Russian range of Capercaillie (Borchtchevski 2007 and unpubl.).

2.2. Data collection and age determination

The study sample comprised Capercaillie cocks killed in 1980–2008 (Table 1) from four different

Table 1. Skulls of Capercaillie cocks from NW Russia used in this study.

Habitat	Area[1]	Description	Sample size	Years of collection
Native	I	Onega' tract	178	1981–1988*
	II	Belomor' tract	43[2]	1990–2008**
Logged	III	Next to Belomor' tract (Figs 1, 2)	240	1999–2008**
	IV	Various sites (23 points, Fig. 1)	61	1980–2001***
Total			522	1980–2008

1) As in Fig. 1.
2) Another 32 were aged according to beak depth (see text).
From: * Borchtchevski 1993, ** Borchtchevski & Sivkov 2010, *** Borchtchevski 2011.

areas (Fig. 1), two in native and two in logged forest. Most were hunted by traditional methods following hunting legislation: in spring at leks and from late August to 1 March by stalking or walking up, with or without barking bird dogs; or at other times under special authorisation (see Borchtchevski 2009) by the same methods. Also, cocks were caught in traps at natural gritting sites in area I, and the remains of birds killed by predators came from all four areas.

The youngest age class (< 12 months old) was determined by feathers and body-dimensions (Semenov-Tian-Shansky 1960). To assign older cocks (≥ 12 months old) to age classes, their skulls were prepared and examined. Age was determined according to generally accepted qualitative criteria: accretion of the *pr. postorbitalis posterior* and *pr. zygomaticus*, of *oo. nasalia* and *oo. frontalia*, ankylosing of the spiral seam between *os dentale* and *os angulare*; plus the state of crests and processes of the skulls of older cocks (Semenov-Tian-Shansky 1960; Moss 1987a; Lindén & Väisänen 1986). Such analysis permits one to distinguish five putative age classes among cocks: 0 = youngest or youngsters of age < 12 months old, 1 = yearlings from 12 to 23 months old, 2 = two-year olds, 3 = three-year olds and 4 = the oldest cocks, aged four or more years.

The most difficult distinction is between two- and three-year olds (Moss 1987a). Nonetheless, as the *os lacrimale* ages it grows in size and changes form: the initially straight juncture between its caudal edge and the *os frontale* curves and approaches step-shaped by 4 years of age (Borchtchevski 2011). This criterion should, however, be used only in combination with others.

In addition, the age of 32 males captured by nets on Capercaillie leks of the Pinega Reserve (point 6, Fig. 2) in 1999–2001, for radio-tagging, was estimated from their beak depth (Moss 1987a, adapted for NW Russian birds by Borchtchevski 2010). This method distinguishes only three age classes: those < 12 months, 12–23 months, and > 23 months. These data were not used in constructing Fig. 3 or the analysis of age structure but were included in analyses of age-specific growth rates.

2.3. Data processing and presentation

2.3.1. Hunting biases and data organisation

In Russia, different methods of hunting Capercaillie cocks show different biases in relation to the birds' age. In spring at leks, hunters shoot mostly old, intensively displaying cocks, and the youngest (< 12 months) birds are under-represented in samples (Teplov 1947, Semenov-Tian-Shansky 1960, Rusanov 1973, Romanov 1979). Conversely, the same authors explain that the youngest birds are over-represented in samples collected by stalking or walking up, with or without the help of barking bird dogs, as young Capercaillie are less cautious and allow a closer approach. Similarly, catching Capercaillie in traps at natural gritting sites also overestimates the proportion of the youngest birds (Shinkin 1967, Romanov 1979, Telepnev 1989). Such biases are quite consistent across regions, habitats and seasons (Teplov 1947, Semenov-Tian-Shansky 1960, Rusanov 1973). We know of no data showing that hunting selects for cocks among older age classes (≥ 12 months) but do not rule out the possibility. For the analysis, we considered different methods of hunting, plus "killed by predator", as separate sampling me-

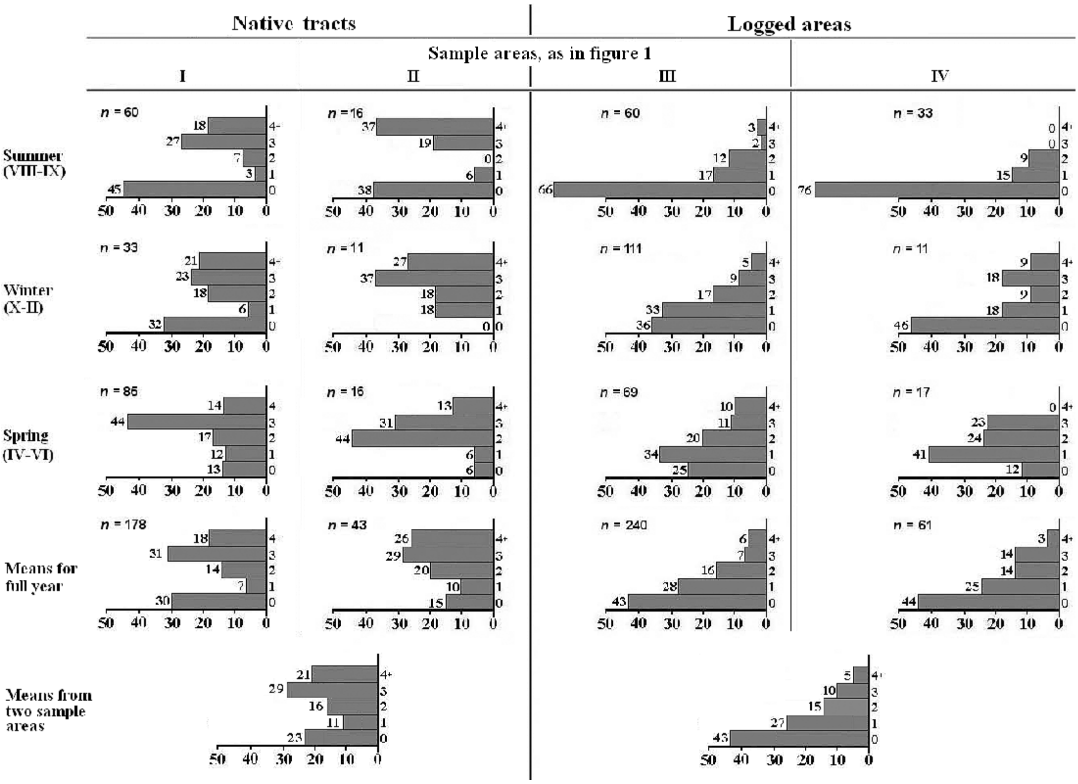

Fig. 3. Age distributions of capercaillie males from NW Russia according to skull collections made during 1980–2008. Vertical axis shows age of males (years), the horizontal one and figures next to columns show relative numbers of birds (%). Samples from: I – Onega' tract, II – Belomor' tract, III – areas next to Belomor' tract, IV – other logged areas (see Fig. 1 and Table 1). Excludes beak depth sample.

thods i.e., shot at lek, netted at lek, trapped at natural gritting sites, walked up with barking bird dog(s), stalked or walked up without dog, and killed by predator.

As sampling biases varied according to season, data for analysis were categorised into three seasons. This ensured that calculations of age-specific annual growth rate (section 2.3.2) between successive age classes were based on pairs of samples, one year different in age, with similar sampling biases:

- "summer" (August and September) – end of the brood period and beginning of the independent life of young Capercaillie;
- "winter" (October–March) – autumn and winter life;
- "spring" (April–June) – from occupation of lek territories to chicks hatching.

The early and middle part of the brood period – from 20 June to 15 August (~ 2 months) – was not covered by our collections.

2.3.2. Age structure and age-specific growth rates

Consider an ideal constant population of N annually breeding birds with $n_{i,t}$ birds aged i years in year t. In horizontal (cohort specific) format:

$$N = n_{0,1} + n_{1,2} + \dots\ n_{i,t} + n_{i+1,t+1} + \dots\ n_{i(f),t(f)} \qquad (1)$$

where $i(f)$ is the age of the oldest surviving age class and $t(f)$ the equivalent year. The population is closed (no immigration or emigration) with constant recruitment ($n_{0,1}$) and each age class has constant survival, although this may differ among age classes. Hence, in vertical (time specific) format:

$$N_t = n_{0,t} + n_{1,t} + \dots n_{i,t} + n_{i+1,t} + \dots n_{i(f),t} \qquad (2)$$

and the survival of each age class can be estimated as the "age-specific annual population growth rate" ($n_{i+1,t} / n_{i,t}$). The average annual survival for the entire population can be calculated as ($1 - n_{0,t} / N_t$). Similarly, the average survival of any segment of the population, comprising all birds aged i and older, can be calculated as ($1 - n_{i,t} / N_{i,t\rightarrow i(f),t)}$), where $n_{i,t} / N_{i,t\rightarrow i(f),t}$ is the number of birds aged i divided by the total of those aged i and older (note $N_t = N_{0,1\rightarrow i(f),t)}$).

In reality, population number, recruitment and survival vary from year to year. Over enough years, however, a random sample from a closed population should have a balanced age distribution that reflects average recruitment and the average survival of each age class in the population. This does not apply if there is immigration or emigration. Age-specific annual population growth rates can nonetheless provide useful information and we estimated these from $n'i$, the number of birds aged i in a sample of N' birds (the dash' signifies a sample, and there is no subscript t because the sample is from many, unspecified years). We called (n'_{i+1} / n'_i) "annual growth rate (method 1)" and ($1 - n'_i / N'_{i\rightarrow i(f)}$), which estimates the average annual growth rate from age i onwards, "average annual growth rate (method 2)".

In method 1, annual growth rates can be > 1 if immigration between ages i and $i + 1$ more than compensates for loss (mortality and emigration) in the same period. Our oldest age class (≥ 4 years old) could comprise birds of several ages and so we did not use it for method 1. In method 2, by definition, average growth rates cannot be > 1.

2.3.3. Statistical analysis

We used logistic regression (numerator/denominator – normally where numerator ≤ denominator) to model age structure and annual growth rates. Skulls were classified according to area (4), season (3) and age class (5), so giving 60 units of analysis (n', shown as individual bars in the three upper rows of Fig. 3). Area, season and age class were also the fixed effects in all three models. For analysis of age structure, the numerator was n' and its denominator the total sample of birds in each season within each area. Preliminary analyses showed the three-way interaction to be insignificant, scarcely affecting the results, and so we consider it no further. For annual growth rate by method 1, some $n'_{i+1} > n'_i$ and so logistic regression could not be used to estimate n'_{i+1} / n'_i directly. We therefore estimated $n'_{i+1} / (n'_i + n'_{i+1})$ and calculated n'_{i+1} / n'_i as $[(n'_{i+1} / (n'_i + n'_{i+1}))] / [1 - (n'_{i+1} / (n'_i + n'_{i+1}))]$. For method 2, we estimated ($n'_i / N'_{i\rightarrow i(f)}$) and subtracted each result from 1.00.

The sample came from different sampling methods, years, and places; thus to allow for sampling heterogeneity, we defined "main sampling method (i)" as the method (section 2.3.1) that contributed most birds to each unit of analysis. Occasionally, there were equal numbers from two or more methods, in which case we included the method combination (e.g., shot at lek & predation) as a separate main method. Each main sampling method was then modelled as a random member of a normally distributed population of main sampling methods, with mean zero. This was done via random effects in Generalised Linear Mixed Models (GLMMs; SAS (2002) Glimmix macro) with binomial distribution and logit link. Degrees of freedom were estimated by Satterthwaite's approximation, which controls for samples with unequal variance (SAS 2004). Temporal heterogeneity was modelled similarly, by including "main year (i)" as a random effect. This was the calendar year that contributed most birds to each unit of analysis. Finally, spatial heterogeneity in annual growth rates was accounted for by including area (I–IV in Table 1) as a random effect.

Analyses of annual growth rate by method 1 (n'_{i+1} / n'_i) involved two units of analysis and so we defined "main sampling method ($i + 1$)" and "main year ($i + 1$)" as additional random effects. This was not done for method 2 because $N'_{i\rightarrow i(f)}$ was the sum of several units of analysis. The GLMMs provided F-tests that gave overall criteria of significance for each fixed effect (area, season, age) and its interactions. Annual growth rates and their 95% confidence limits were calculated from the models' predictions and their standard errors. To compare a pair of annual growth rates we inspected their means and confidence limits. When confidence intervals did not overlap, the difference was statistically significant ($P < 0.05$). To calculate exact probabilities in critical cases, we tested the difference by simulation tests. In effect, we reconstituted normal distributions from the two model predictions and their standard errors, took a random sample from each distribution, and calculated their ratio. We repeated this 10,000 times and ranked the resulting ratios. The two-tailed probability (P) of the observed difference occurring by chance was the rank at which the ratio was closest to unity, divided by 5,000. To compare several (q) pairs of values we compared each pair as above and then combined the estimated probabilities (P) according to $-\Sigma \ln P$, which is distributed as χ^2 with $2q$ degrees of freedom (Fisher 1925).

3. Results

3.1. Age structure

Collation of all skull samples shows noticeable differences in age structure (Fig. 3), mostly between native (I & II) and logged (III & IV) areas. Native forest had an unbalanced age structure with a relative excess of 2- and 3-year-old males (45 & 49%, both ages combined) and a corresponding deficiency of the youngest and yearling birds (25 & 37%). Logged forest, by contrast, showed a more or less balanced age structure with fewer 2- and 3-year-old males (23 & 28%) and more younger ones (69 & 71%), except in spring when the sample came largely from birds shot at leks (section 2.3.1).

The GLMM analysis of age structure included “main sampling method” and “main year” as random effects. The covariance parameter estimate for main year was ≤ 0, which meant that main year did not modify the results calculated solely from fixed effects. Also, the covariance parameter estimate for main sampling method was small at 0.073. This implied that the fixed effect “season” accounted for most of the sampling bias, as intended (section 2.3.1).

SAS type 1 (sequential) F-tests showed no significant differences among areas ($F_{3,1} = 0.93$, $P = 0.62$) or seasons ($F_{2,1} = 1.10$, $P = 0.56$) when entered as main effects, but significant differences among age classes ($F_{4,20} = 19.2$, $P < 0.0001$). The area × season interaction ($F_{6,1} = 0.38$, $P = 0.84$) was not significant, but age × season ($F_{8,20} = 10.34$, $P < 0.0001$) and age × area ($F_{12,20} = 7.35$, $P < 0.0001$) were. Thus age structure differed significantly among seasons and among areas.

Table 2. Age structure of capercaillie skull samples from four areas in NW Russia: parameter estimates for the area × age interaction from a GLMM (logit link, binomial distribution), expressed as differences from area IV and age class 4. Bold font highlights the main differences between logged and native habitat after controlling for season and sampling method: fewer birds of age classes 0 and 1 in native habitat.

Habitat	Area (Fig. 1)	Age class	Estimate	Standard error
Native	I	0	**–1.48**	1.27
	I	1	**–2.08**	1.28
	I	2	–0.76	1.29
	I	3	0.13	1.30
	I	4	0	–
	II	0	**–2.57**	1.40
	II	1	**–2.40**	1.43
	II	2	–0.66	1.39
	II	3	–0.59	1.39
	II	4	0	–
Logged	III	0	**0.37**	1.25
	III	1	**0.63**	1.24
	III	2	0.69	1.27
	III	3	–0.47	1.30
	III	4	0	–
	IV	0	**0**	–
	IV	1	**0**	–
	IV	2	0	–
	IV	3	0	–
	IV	4	0	–

We knew that age class 0 was over-sampled in summer and under-sampled in spring, and so the age × season interaction above was presumably due largely to sample biases in age class 0. To check this, we repeated the analysis without age class 0 and entered the age × season interaction into the model last. It was now insignificant ($F_{6,15} = 0.96$, $P = 0.49$). This suggests that any seasonal sampling bias had little impact on the age distribution of birds in age classes 1–4.

The main differences in age structure, after controlling for season (fixed effect) and sampling method (random effect), were between native and logged areas (Table 2). Hence it was reasonable to categorise data as coming from native or logged areas when calculating annual growth rates.

Table 3. Annual age-specific growth rates of Capercaillie cocks from NW Russia calculated by method 1. Estimates and 95% confidence intervals (95% CI) are reported for native and logged habitats.

Age[1]	Season	Native habitat		Logged habitat	
		Estimate	95% CI	Estimate	95% CI
0 (2–11)	Summer	0.15	0.05–0.41	0.22	0.11–0.44
	Winter	0.26	0.08–0.81	0.68	0.32–1.46
	Spring	1.09	0.55–2.17	1.94	0.99–3.86
1 (14–23)	Summer	**2.71**[2]	0.72–10.2	0.62	0.25–1.53
	Winter	**1.41**	0.50–4.02	0.58	0.30–1.13
	Spring	**2.25**	1.02–4.97	0.62	0.31–1.26
2 (26–35)	Summer	**2.08**	0.72–6.00	0.53	0.15–1.85
	Winter	**1.33**	0.51–3.43	0.61	0.25–1.45
	Spring	**1.89**	0.88–4.04	0.58	0.26–1.27

1) As in Fig. 3 (age in months). Growth rates are prospective.

2) The estimates in bold are all > 1.00 but only one (age 1, spring) significantly so. A combined simulation test (see section 2.3.2) for the null hypothesis $H_0 = 1$, however, gave $\chi^2_{12} = 23.4$, $P = 0.024$.

3.2. Annual growth rates in native *vs* logged areas

3.2.1. Sampling biases

Sampling method was a likely source of bias. Dividing the data into three seasons (section 2.3.1) was intended to control for this. Nonetheless, we entered "main sampling method (i)" and "main sampling method ($i + 1$)" as random effects (section 2.3.3) in the GLMM for method 1 and "main sampling method (i)" in that for method 2. Covariance parameter estimates were ≤ 0 in each case. As for age structure (section 3.1), this confirmed that dividing the data into seasons controlled well for biases due to sampling method.

Year of sampling was another potential source of bias. The GLMM for method 1 included main year (i) and main year ($i + 1$) as random effects, but estimated the covariance for main year (i) to be ≤ 0. The covariance parameter estimate for main year ($i + 1$) was small at 0.074. The GLMM for method 2 included main year (i) as a random effect and estimated its covariance parameter at 0.046. In short, the GLMMs corrected for biases due to year of sampling, but the corrections were small.

Place of sampling was a third potential source of bias. "Main year" (previous paragraph) inevitably involved much spatial as well as temporal heterogeneity. Nonetheless we ran the GLMMs with "area" as an additional random effect. Its covariance estimate was ≤ 0. Hence main year accounted for both spatial and temporal heterogeneity.

3.2.2. Annual growth rate (method 1)

Just as age structure differed between native and logged areas (Fig. 3, Table 2), so did annual growth rates estimated by method 1 (Table 3). For the GLMM, we categorised areas I & II as native habitat and areas III & IV as logged habitat. The main effects habitat (SAS type 3 (partial) F-test: $F_{1,16.4} = 4.83$, $P = 0.043$), season ($F_{2,19} = 4.23$, $P = 0.030$) and age ($F_{2,19} = 5.60$, $P < 0.012$) were significant.

The habitat × season interaction ($F_{2,19} = 0.49$, $P = 0.62$) was not significant, which means that differences among seasons were similar in the two habitats.The season × age interaction ($F_{4,29} = 4.45$, $P = 0.010$) was however significant, evidently (Table 3) due to big seasonal differences in age class 0 (section 3.1).

Crucially, the habitat × age interaction ($F_{2,19} = 8.14$, $P = 0.0028$) demonstrated age-related significant differences in annual growth rates between habitats. In particular, growth rates for 2- and 3-year-olds are all > 1 for native habitat, consistent with immigration into native habitat (Introduction).

3.2.3. Average annual growth rate (method 2)

This method (Table 4) estimates average annual

Table 4. Average annual age-specific growth rates of Capercaillie cocks from NW Russia calculated by method 2. Estimates and 95% confidence intervals (95% CI) are reported for native and logged habitats.

Age[1]	Season	Native habitat		Logged habitat	
		Estimate[2]	95% CI	Estimate	95% CI
0 (2–11)	Summer	**0.62**[3]	**0.49–0.74**	**0.28**	**0.20–0.37**
	Winter	0.77	0.61–0.87	0.60	0.45–0.74
	Spring	0.87	0.79–0.92	0.80	0.70–0.88
1 (14–23)	Summer	**0.91**	**0.80–0.96**	**0.49**	**0.32–0.67**
	Winter	**0.87**	**0.75–0.94**	**0.55**	**0.41–0.68**
	Spring	**0.82**	**0.73–0.88**	**0.53**	**0.40–0.66**
2 (26–35)	Summer	**0.80**	**0.62–0.91**	**0.35**	**0.17–0.58**
	Winter	**0.77**	**0.61–0.88**	**0.46**	**0.31–0.61**
	Spring	0.73	0.60–0.83	0.48	0.32–0.64
3 (38 +)	Summer	0.53	0.36–0.70	0.36	0.14–0.64
	Winter	0.43	0.25–0.64	0.41	0.22–0.62
	Spring	0.30	0.18–0.45	0.35	0.18–0.56

1) As in Fig. 3 (age in months).
2) Estimates are the average for the focal and all older age classes. Estimates on the same line are significantly different ($P < 0.05$) if confidence intervals do not overlap (bold type).
3) Difference Native *vs* Logged by simulation test (see text) $P < 0.001$.

growth rates for all birds in the focal and older age classes. The results are therefore weighted in favour of the most numerous age classes. Confidence intervals are narrower than for method 1, partly because sample sizes are bigger and partly because, by definition, average growth rate cannot be > 1.

The main effects habitat (SAS type 3 (partial) F-test: $F_{1, 20.5} = 31.2$, $P < 0.0001$) and age ($F_{3, 29} = 10.6$, $P < 0.0001$) were significant but season ($F_{2, 29} = 1.05$, $P = 0.36$) was not. As for method 1 (previous section), the habitat × season interaction ($F_{2, 29} = 3.20$, $P = 0.056$) was not significant, but the season × age interaction was ($F_{6, 29} = 5.91$, $P = 0.0004$). Again, the habitat × age interaction ($F_{3, 29} = 3.91$, $P = 0.018$) demonstrated significant age-related differences in growth rate between habitats.

Average annual growth rate for birds < 12 months was equivalent to the term $1 - y$ (where y is the proportion of young in sample), and was lower on logged than on native habitat – especially in summer. This in turn was because the summer logged sample had a higher proportion (72% *vs* 38%, equivalent to 2.6 young / old *vs* 0.6 young / old) of young birds (< 4 months). As for method 1 (Table 3), the annual average growth rates of birds in age classes 1 (and older) and 2 (and older) were higher on the native area (Table 4), consistent with stream 2 of the two-compartment model (Introduction).

Average annual growth rate of birds aged ≥ 38 months was, however, very similar in native and logged areas, especially in winter and spring. In this case, therefore, there was no evidence of movement between native and logged areas. Hence, assuming the two-compartment model, the average growth rate for this age class should be a realistic estimate of their average survival.

4. Discussion

4.1. Sampling biases

Our conclusions depend on the age structures of samples from logged and native forest being representative. The unbalanced sample from native forest was salient. Unrepresentative or unbalanced age distributions can arise if samples are taken at particular stages of a population fluctuation, but for area I unbalanced distributions occurred in each year of collection (Borchtchevski 1990, 1993). Unrepresentative sampling can similarly be ruled out for areas II and III (Borchtchevski & Sivkov 2010). In the case of area IV, the immense area and large number of years involved makes it likely that the sample is reasonably representative (Borchtchevski 2011).

In GLMMs, biases associated with the method of sampling were largely controlled by dividing the data into seasons, as confirmed by the good agreement among seasons within age classes (see sections 3.1, 3.2, Tables 3 and 4). The exception was the youngest age class, for which sampling biases evidently contributed to the differences among seasons. These included (see section 2.3.1) biases towards birds < 12 months in summer and winter, which would depress estimates of annual growth rate; and against such birds in spring, which would increase estimates. Residual biases associated with method, year or place of sampling were corrected by modelling them as random effects.

4.2. Ageing skulls

The most difficult distinction to make when classifying skulls is between age classes 2 and 3 (section 2.2). Random misclassification of skulls in these two age classes would tend to equalise the numbers in each, so depressing the annual growth rate of 2-year-olds in balanced samples and increasing it in unbalanced ones. Conversely, it would increase the growth rate of 3-year-olds in balanced samples and depress it in unbalanced ones. In the event, we treat 2- and 3-year-olds together as part of movement stream 2 (Introduction) and so this putative misclassification error is inconsequential for the conclusion that movement can explain the observed age ratios.

The same error would impact growth rates of the oldest birds (method 2 only), causing observed values to be somewhat higher than real ones on logged areas and lower in native forest. This is discussed in section 4.4.

4.3. Age structure and movements

Age structure (see section 3.1) was unbalanced in both native tracts studied (samples I & II) but more or less balanced over the vast adjacent logged areas (samples III & IV). The relative excess of 2- and 3-year-old males on native tracts resulted in annual growth rates (method 1, Table 3) significantly > 1 there. This strongly suggests immigration, consistent with stream 2 of the two-compartment hypothesis (Introduction).

Evidence consistent with stream 1 (Introduction) includes the discrepant ratios of newly-reared youngsters to older birds in summer samples from logged and native tracts (2.6 *vs* 0.6 young / old, section 3.2.3). In the absence of movement, this might imply very much better reproduction on the logged area. Or the bias towards shooting youngsters might have been bigger in logged forest. An alternative explanation is net immigration of young birds from native into logged forest (stream 1, Introduction). Another possibility is emigration of old birds from logged into native forest (stream 2, Introduction) although this seems unlikely in late summer or early autumn (section 4.5). The idea that these discrepant ratios reflect movement goes along with Borchtchevski's (1993) observations of sudden declines in Capercaillie density on area I (Fig. 1) from an average ~ 5 birds / km^2 in September to only ~ 2 birds / km^2 in November. He estimated that mortality explained only 13% of the average decline.

Such movements may be over long distances. Thus, almost the entire sample from area I (Fig. 1) was collected in the centre of the Onega' tract and, during the period of data collection, the shortest distance from its centre to the nearest clear-cuts was 80–100 km. The distribution of samples inside the Belomor' tract (area II) was more uniform (Fig. 2) but nonetheless inside its boundaries – some males would have had to move 40–60 km between logged areas and the central part of the tract. Such distances are in accord with the literature on this region (Introduction).

4.4. Annual growth rates and survival

In our ideal population (section 2.3.2), age-specific annual population growth rate is the same as age-specific annual survival. Average annual survival of radio-tagged cocks > 12 months old, in studies outside Russia, includes estimates of 0.77 in Norway, 0.70 in the Pyrenees, 0.81 in Scotland and 0.84 in the Bavarian Alps (Storch 2001). These values are similar to average annual growth rates for birds in native forest from 14–35 months of age (mean 0.82, method 2, Table 4), but comparable growth rates in logged forest are much lower (0.48). We argue that this is due to net movement from logged to native forest and hence our values do not measure survival.

The annual growth rate (Table 4) of birds > 3 years, however, was very similar in native and logged areas (0.42 and 0.37 respectively), which suggests little or no net movement between habitats. Hence, assuming the two-compartment model, about 0.40 should be a realistic estimate of survival, unless there was a large sampling bias against older, warier birds. This would require that birds > 3 years were only half as likely to be sampled as 3-year-olds on both native and logged areas, which seems unlikely. Another caveat is the possibility (section 4.2) of misclassifying age classes 2 and 3. In any case, an average of about 40% annual survival was plainly very much lower than expected from the literature. This evidence points to a sudden increase in annual mortality when birds reached the age (> 3 years) at which they usually start trying to establish themselves as alpha cocks.

In different conditions, Capercaillie cocks attain breeding status at different ages: at very small leks cocks may mate in their second spring (V. Borchtchevski, unpubl.), whereas on large leks (> 30 displaying cocks) with much competition there is evidence that breeding cocks may not first mate until their fifth spring (Dronseiko & Nemnonov 1984). Displaying cocks are hunted by men and killed by predators as well as fighting to the death amongst themselves. Hunting seems an unlikely cause of excess mortality amongst mature cocks in native areas because these were remote and people sparse (next section), but hunters might have killed many old birds on logged areas. Predation is likely, especially if experienced cocks suffer much heavier predation than less mature ones after being injured in fights. Fights between displaying cocks may be to the death, or a bird may be so injured that it becomes more vulnerable to predators (Borchtchevski 1993), or it may die from its wounds after a fight.

4.5. Timing and causes of movements

Stream 1, emigration in September–November, can be seen as dispersal of mostly young birds. Stream 2, however, involves a return movement of 2- and 3-year-old birds moving from lower to higher densities, presumably attracted by native habitat or the much bigger and more frequent leks in such habitat (Introduction).

High apparent mortality of cocks > 3 years old could result from continued attempts of birds to move out of logged areas and establish themselves as alpha cocks in native forest. At high population density, intense competition for alpha status could well result in heightened frequency and intensity of conflicts, and consequent high mortality. This is consistent with the idea that movements from logged to native forest are driven by a struggle for territories at big leks. In addition, the greater frequency of people recorded during spring transect counts of birds in logged than in native areas (5.3 *vs* 0.1 persons / 100 km, Borchtchevski 2011 and unpubl.) made the latter more attractive due to very low disturbance and hunting pressure. All this raises the question of when stream 2 occurs.

It is difficult to envisage such movement in late summer or early autumn, when the moult of old cocks is under way. Some cocks could emigrate from native forest to moult in dense logged habitats after the display period, but one would expect them to return to their leks not in autumn but in spring (Hjeljord *et al*. 2000). Over winter, to avoid predation Capercaillie males must either join large flocks or avoid concentrating in high densities: but large winter groups of Capercaillie were not typical of the region during our study. Some small flocks (3–5 birds) were recorded, but the majority of cocks wintered alone (V. Borchtchevski unpubl.).

This argues against large-scale movements from logged to native forest during winter. So do count data collected in area I (Fig. 1) throughout the annual cycle: these showed no increase of Capercaillie density from August to March, but density did increase in April (Borchtchevski 1993). None of the above considerations is conclusive but together they point to stream 2 occurring mainly in spring.

All cocks > 10 months could find native forest attractive. But high spring density of older Capercaillie in optimal native forest may provoke heightened aggressiveness in old cocks. Thus, as a cock matures, its social status increases (Dronseiko & Nemnonov 1984). After lekking in the early morning, each mature cock occupies an individual daytime territory and avoids other territorial males – although daytime territories around big leks can overlap and the behaviour of a territory owner towards an intruder depends upon the latter's status (Eliassen & Wegge 2007). This behaviour handicaps the establishment of younger cocks and may even impede their movement through areas with regularly spaced leks and a high density of fully mature males. Younger males attempting to establish themselves in optimal native habitat may be forced back to logged areas or retreat into patches of poor habitat inside native tracts. This might continue during an aspiring immigrant's second, third, or even fourth year of life – until he can overcome the aggressive resistance of resident males in spring.

Such attempts of younger males from logged forest to establish themselves at the large leks of native areas could impart a seasonal character to Capercaillie movements: in late summer (after brood break up) and autumn – dispersal from native to logged areas, in spring – in the opposite direction. The nature of such migrations must differ fundamentally from that proposed for coarse-grained landscape mosaics (Rolstad & Wegge 1989), because we suggest that spring migration heralds attempts by younger cocks to establish themselves in native areas.

Such movements could be documented with marked birds. However, the two radio-tagging studies in the region, at the Pinega Reserve (point 6, Fig. 2) (Hjeljord *et al*. 2011) and Pechora-Illych Reserve (point PI, Fig. 1) (Beshkarev *et al*. 1995), did not show long movements. Catching was done at the lek in spring and so too late to sample stream 1 (autumn emigration). Any stream 2 (spring immigration from logged areas) birds would already have arrived at their destination. Hence, the fact that no long movements were discovered (Wegge *et al*. 2003, 2005, Hjeljord *et al*. 2011) was to be expected from the hypothesis.

Movements into native tracts could also be amplified by the destruction of leks and habitat due to permanent logging on their periphery (Borchtchevski & Sivkov 2010). The distances moved by such refugees are not known. A possible example may be movements of Capercaillie into Finland due to the logging of Karelian forests in the last century (Brüll 1965). Nonetheless, long movements of large numbers of Capercaillie were repeatedly recorded in areas where there were no big clear-cuts (by lake Baikal, in the Yenisei and Lena river basins) or before large clear-cuttings had started (the Pechora river basin) (Potapov 1985).

4.6. Capercaillie population dynamics and movement

From the age structure of Capercaillie shot and found dead in Scottish woodland in the 1970s and 1980s, Moss (1987b) inferred net emigration of yearling (age class 1) cocks from dense (~ 10 birds / km^2 in spring) populations of Capercaillie in old Scots pine forests to surrounding woodland habitat of poorer quality. Also, the average annual growth rate for age classes 1–4 in old forest was 0.55, much lower than the 0.81 annual survival subsequently documented from radio-tagged birds (Moss *et al*. 2000). This would be expected if total losses from old forest comprised mortality plus net emigration. From counts in one high-density forest, Moss & Oswald (1985) inferred that breeding densities were determined by losses and gains involving emigration and immigration.

In addition, our results are consistent with Norwegian data showing age-dependent population segregation: there, the youngest Capercaillie males were more abundant in logged habitats, where survival was lower (Wegge *et al*. 1990).

There are big differences between Scotland, Norway and NW Russia, not least the much larger spatial scale of Russian forest. Also the number of Capercaillie in Scotland declined roughly tenfold between the 1970s and the end of the 20th century (Ewing *et al*.2012) so past patterns of movement may no longer occur. Nonetheless, two-way movement seems to have been an important determinant of densities and age structure in each of these three situations.

4.7. Conclusions

The forest of NW Russia comprises a greatly-contrasting, coarse-grained mosaic of two habitat types: patches of native forest set within a large and fairly uniform area of logged forest with few natural barriers. The age structure of male Capercaillie is balanced in logged areas with low population density, where leks are sparse and mostly small; but an unbalanced structure is typical of native forest with higher population density and regularly spaced leks, including large ones. We infer that this is due to two streams of movement: 1) dispersal of mostly young birds, from native to logged forest; and 2) a return movement mostly of 2- and 3-year-old birds from logged to native areas, presumably attracted by native habitat or the much bigger leks in such habitat. This is consistent with the Capercaillie of NW Russia comprising a single "super-population" united by long-distance movements between patches of native forest and the much bigger area of logged forest that surrounds them.

In addition, the data indicate a remarkable decrease in the survival of cocks over 3 years old. We speculate that this is due to attempts of such birds to establish themselves as alpha cocks in native forest. This implies that the number of alpha cocks is limited, presumably by density and habitat, such that in native forest most cocks aged 2–3 years comprise a "population reserve". Until recently, native forest has been quite inaccessible to hunters and so its inferred role in generating a population reserve has been preserved. Now, however, hunters are gaining greater access and Capercaillie in native forest are being regarded as a hunting resource. The two-way migration postulated here, and its presumed underlying agonistic interactions, may apply only when the entire NW Russian super-population is at high density. As such super-populations become fragmented into isolated populations, such as those in Western Europe (Duriez *et al*. 2007, Segelbacher & Piertney 2007, Bajc *et al*. 2011), long-distance two-way migration must become less feasible. Hence there should be no population reserve of middle-aged birds, as also noted for most bird species in the north of Western Siberia (Ryabitsev1998), where Capercaillie density is low (0.03–0.09 birds/km^2, Korkina & Ravkin 2011, V. Borchtchevski unpubl.) and the age structure of cocks is balanced (Borchtchevski & Kupriyanov 2010).

Acknowledgements. Many thanks to Dr. A. Lindén, the associate editor and three anonymous referees for constructive criticisms of preliminary versions of the manuscript.

Metsokukkojen (*Tetrao urogallus*) ikäjakauma Luoteis-Venäjällä saattaa heijastaa kaksisuuntaista liikehdintää

Luoteis-Venäjällä vuosina 1980–2008 kerätyt metsokukkojen kallot, noudattivat kahta erilaista ikäjakaumaa. Alkuperäisessä metsässä ja suometsässä, jossa metsotiheys oli suuri (keväällä ~ 2.0 lintua / km^2) oli suhteessa enemmän 2- ja 3-vuotiaita koiraita, ja vastaavasti vähemmän vuoden ikäisiä lintuja. Päinvastainen tilanne vallitsi laajalti hakatuilla alueilla, jossa metsotiheys oli matalampi (~ 0.6 lintua / km^2). Näillä oli siis vähemmän 2- ja 3-vuotiaita ja enemmän nuorempien ikäluokkien edustajia.

Tulokset tukevat hypoteesiä, että nuoret koiraat muuttavat hakkuualueille, kun taas vanhenevilla kukoilla on toisensuuntaista liikehdintää, yrittäen liittyä suuriin soitimiin jotka sijaitsevat luonnonvaraisissa metsissä. Tulokset viittaavat myös siihen, että yli 3-vuotiaiden kukkojen selviytyvyys on matala molemmissa habitaattityypeissä, mahdollisesti johtuen jatkuvasta muutosta hakatuilta alueilta, yhdistettynä kovaan kilpailuun suurilla soitimilla. Moiset liikehdinnät tapahtuvat otaksuttavasti lähinnä niinä ajankohtina kuin populaatiotiheydet ovat korkeita.

References

Aksenov, D., Dobrynin, D., Dubinin, M., Egorov, A., Isaev, A., Karpachvskiy, M., Lestadius, L., Potapov, P., Purekhovskiy, A., Turubanova, S. & Yaroshenko, A. 2002: Atlas of Russia's intact forest landscapes. — Global Forest Watch, Moscow.

Bajc M., Čas, M., Ballian, D., Kunovac, S., Zubić, G., Grubešić, M., Zhelev, P., Paule, L., Grebenc, T. & Kraigher, H. 2011: Genetic differentiation of western capercaillie highlights the importance of South-Eastern Europe for understanding the species phylogeography. — PloS ONE: 6(8): e23602. doi:10.1371/journal.pone.0023602.

Beshkarev, A.B., Blagovidov, A., Teplov, V. & Hjeljord, O. 1995: Spatial distribution and habitat preference of male capercaillie in the Pechora-Illych Nature Reserve in 1991–92. — In Proceedings of the 6th International Grouse Symposium (ed. Jenkins, D.): 48–53. World Pheasant Association & Instituto Nazionale per la Fauna Selvatica. Udine, Italy.

Borchtchevski, V.G. 1990: Age composition of the territorial grouping of capercaillie (*Tetrao urogallus*) in the west of the Arkhangelsk region. — Zoological Journal (Moscow) 69: 94–104. (In Russian with English summary)

Borchtchevski, V.G. 1993: Population biology of the capercaillie. Principles of the structural organisation. — Central Science Laboratory of Game Management and Nature Reserves, Moscow. (In Russian with English summary)

Borchtchevski, V.G. 2003: Joint habitat use by four grouse species (*Tetrao urogallus, Tetrao tetrix, Bonasa bonasia, Lagopus lagopus*) in the Vodlozersky National Park (NW Russia) during early spring. — In Dynamics of game animal populations in Northern Europe: Proceedings of the 3rd International Symposium (eds Danilov, P.I. & Zimin, V.B.): 26–31. Petrozavodsk.

Borchtchevski, V.G. 2007: Large-scale analysis of grouse distribution in Northwestern Russia. — In Dynamics of game animal populations in Northern Europe: Proceedings of the 4th International Symposium (ed. Danilov, P.I.): 37–47. Petrozavodsk. (In Russian with English summary)

Borchtchevski, V.G. 2009: The May diet of Capercaillie (*Tetrao urogallus*) in an extensively logged area of NW Russia. — Ornis Fennica 86: 18–29.

Borchtchevski, V.G. 2010: Determining the age of capercaillie (*Tetrao urogallus*) by the beak depth in Northwestern Russia. — Bulletin of Game Management 7: 75–81. (In Russian with English summary)

Borchtchevski, V.G. 2011: The age composition of capercaillie *Tetrao urogallus* in logged areas of NW Russia. — Russian Ornithological Journal 20: 2059–2076. (In Russian)

Borchtchevski, V.G. & Kuprianov, A.G. 2010: Age composition of capercaillie (*Tetrao urogallus*, Tetraonidae, Galliformes) population in the northern part of Western Siberia. — Zoological Journal (Moscow) 89: 609–619. (In Russian with English summary)

Borchtchevski, V.G. & Sivkov, Ŕ.V. 2009: Does the capercaillie (*Tetrao urogallus*) clutch size is density dependent? — Bulletin of Game Management 6: 119–131. (In Russian with English summary)

Borchtchevski, V.G. & Sivkov, A.V. 2010: Age composition of the capercaillie (*Tetrao urogallus*) population in north of the Arkhangelsk region. — Bulletin of Game Management 7: 82–97. (In Russian with English summary)

Brüll, H. 1965: Zur hege und hegegerechten bejagung des birkwildes. — Österreichs Weidwerk 4: 44–147. (In German)

Couturier, M. & Couturier, A. 1980: Les coqs de bruyère. Vol. 1: Le grand coq de bruyère *Tetrao urogallus urogallus* L. — F. Dubusc, Boulogne. (In French)

Cramp, S. & Simmons, K.E.L. 1980: Handbook of the birds of Europe, the Middle East and North Africa: The birds of the western Palearctic, Vol. 2. — Oxford University Press, Oxford.

Dronseiko, E.G. & Nemnonov, N.N. 1984: The capercaillie lek. — In Proceedings of International Conference on Capercaillie: 42–55. Ed. Rosselkhozizdat, Moscow. (In Russian)

Duriez, O., Sachet, J.-M., Ménoni, E., Pidancier, N., Miquel, C. & Taberlet, P. 2007: Phylogeography of the capercaillie in Eurasia: what is the conservation status in the Pyrenees and Cantabrian Mountains? — Conservation Genetics 8: 513–526.

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

Ewing, S.R., Eaton, M.A., Poole, T.F., Davies, M. & Haysom, S. 2012: The size of the Scottish population of Capercaillie *Tetrao urogallus*: results of the fourth national survey. — Bird Study 59: 126–138.

Fisher, R.A. 1925: Statistical methods for research workers. — Oliver and Boyd, Edinburgh.

Hjeljord, O., Wegge, P., Rolstad, J., Ivanova, M. & Beshkarev A.B. 2000: Spring–summer movements of male capercaillie *Tetrao urogallus*: A test of the “landscape mosaic” hypothesis. — Wildlife Biology 6: 251–256.

Hjeljord, O., Wegge, P. & Sivkov, A.V. 2011: Research on Russian grouse. — Grouse news 42: 7–13.

Kirikov, S.V. 1952: Birds and mammals in conditions of landscapes of the southern extremity of the Urals. — Ed. Nauka, Moscow. (In Russian)

Korkina, I.P. & Ravkin, Y.S. 2011: Experience of geoinformation technology application for cartographical display of population number and dispersal of the capercaillie on the West- Siberian plain. — Bulletin of Tomsk State University. Biology 4: 54–59. (In Russian)

Kuzmina, M.A. 1968: Distribution and numbers of grouse in Kazakhstan. — In Resources of grouse in USSR: 45–47. Ed. Nauka, Moscow. (In Russian)

Lindén, H. 1988: Latitudinal gradients in predator-prey interactions, cyclicity and synchronism in vole and small game populations in Finland. — Oikos 52: 341–349.

Lindén, H. 1989: Characteristics of tetraonid cycles in Finland. — Finnish Game Research 46: 34–42.

Lindén, H. & Väisänen, R.A. 1986: Growth and sexual dimorphism in the skull of the capercaillie *Tetrao urogallus*: a multivariate study of geographical variation. — Ornis Scandinavica 17: 85–98.

Lindström, J., Ranta, E., Lindén, M., Lindén, H. 1997: Reproductive output, population structure and cyclic dynamics in capercaillie, black grouse and hazel grouse. — Journal of Avian Biology 28: 1–8.

Liukkonen-Anttila, T., Rätti, O., Kvist, L., Helle, P. & Orell, M. 2004: Lack of genetic structuring and subspecies differentiation in the capercaillie (*Tetrao urogallus*) in Finland. — Annales Zoologici Fennici 41: 619–633.

Melekhov, I.S., Korkonosova, L.I. & Chertovskoy, V.G. 1965: Guidance on the study of the concentrated loggings. — Ed. Nauka, Moscow. (In Russian)

Moss, R. 1987a: Demography of capercaillie *Tetrao urogallus* in north-east Scotland. I. Determining the age of Scottish capercaillie from skull and head measurements. — Ornis Scandinavica 18: 129–134.

Moss, R. 1987b: Demography of capercaillie *Tetrao urogallus* in north-east Scotland. II. Age and sex distribution. — Ornis Scandinavica 18: 135–140.

Moss, R. & Oswald, J. 1985: Population dynamics of capercaillie in a north-east Scottish glen. — Ornis Scandinavica 16: 229–238.

Moss, R., Picozzi, N., Summers, R.W. & Baines D. 2000: Capercaillie *Tetrao urogallus* in Scotland – demography of a declining population. — Ibis 142: 259–267.

Moss, R. & Weir, D.N. 1987: Demography of capercaillie *Tetrao urogallus* in north-east Scotland. III. Production and recruitment of young. — Ornis Scandinavica 18: 141–145.

Potapov, R.L. 1985: Order Galliformes, Family Tetraonidae. — In Fauna of the USSR: birds, Vol. 3. Ed. Nauka, Leningrad. (In Russian)

Pulliam, H.R. 1988: Sources, sinks, and population regulation. — American Naturalist 132: 652–661.

Rolstad, J. & Wegge, P. 1989: Capercaillie *Tetrao urogallus* populations and modern forestry – a case for landscape ecological studies. — Finnish Game Research 46: 43–52.

Rolstad, J., Wegge, P., Sivkov, A.V., Hjeljord, O. & Storaunet, K.O. 2009: Size and spacing of grouse leks: comparing capercaillie (*Tetrao urogallus*) and black grouse (*Tetrao tetrix*) in two contrasting Eurasian boreal forest landscapes. — Canadian Journal of Zoology 87: 1032–1043.

Romanov, A.N. 1979: The common capercaillie. — Ed. Nauka, Moscow. (In Russian)

Rusanov, Y.S. 1973: Hunting and protection of fauna (Influence of hunting on the population structure of hunted animals). — Ed. Forestry, Moscow. (In Russian)

Ryabitsev, V.K. 1998: Territorial relations and community dynamics of birds in the Subarctic. — Ed. Nauka, Ekaterinburg. (In Russian)

SAS 2002: Glimmix macro to fit the generalized linear mixed model. — SAS Institute Inc., Cary, NC. Available at: http://support.sas.com/kb/25/030.html (Last accessed 23 06 2012).

SAS 2004: SAS/STAT 9.1 User's Guide. — SAS Insitute Inc., Cary, NC.

Segelbacher, G. & Piertney S. 2007: Phylogeography of the European capercaillie (*Tetrao urogallus*) and its implications for conservation. — Journal of Ornithology 148 (Suppl 2): 269–274.

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

Shinkin, N.A. 1967: Gallinaceous birds of the south-eastern part of Western Siberia – their economic use and protection. — Thesis, Tomsk. (In Russian)

Siivonen, L.1952: On the reflection of short-term fluctuations in numbers in the reproduction of tetraonids. — Papers on Game Research 9: 1–43.

Storch, I. 2001: Capercaillie. — BWP Update 3: 1–24.

Telepnev, V.G. 1989: Sexual and age structure of capercaillie population and factors influencing its change in Western Siberia. — In Ecology and resources of hunting birds. (ed. Litun, V.I.): 42–49. Kirov. (In Russian)

Teplov, V.P. 1947: Capercaillie in Petchoro-Ilich Reserve. — Transactions of the Petchoro-Ilich State Reserve (Moscow) 4: 3–76. (In Russian)

Wegge, P., Gjerde, I., Kastdalen, L., Rolstad, J. & Storaas T. 1990: Does forest fragmentation increase the mortality rate of capercaillie. — Transactions of 19th IUGB Congress (ed. Myrberget, S): 448–453. Nina, Trondheim.

Wegge, P., Kvålsgard, T., Hjeljord, O. & Sivkov, A.V. 2003: Spring spacing behaviour of capercaillie *Tetrao urogallus* males does not limit numbers at leks. — Wildlife Biology 9: 283–289.

Wegge, P. & Larsen, B.B. 1987: Spacing of adult and subadult male common capercaillie during the breeding season. — Auk 104: 481–490.

Wegge, P., Olstad, T., Gregersen, H., Hjeljord, O. & Sivkov, A.V. 2005: Capercaillie broods in pristine boreal forest in northwestern Russia: the importance of insects and cover in habitat selection. — Canadian Journal of Zoology 83: 1547–1555.