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Lack of genetic structuring and subspecies differentiation in the capercaillie (*Tetrao urogallus*) in Finland

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We sequenced and analysed variation in a 430 bp segment of the mitochondrial DNA control region of 302 Finnish capercaillies *Tetrao urogallus*. The data were divided into four zones representing the three suggested subspecies (*T. u. urogallus*, *T. u. uralensis*/*karelicus*, *T. u. major*), and the zone for hybrids between *T. u. urogallus* and *T. u. uralensis*. We did not find any clear evidence for different subspecies zones, or for differentiation among local populations. One major haplotype dominated in three zones and comprised 46% of all the sampled birds, and variation among individuals explained 98% of the total variance. Nucleotide and haplotype diversities tended to be high in northern and central parts of the country, whereas lower values were found at the west cost and in eastern parts of the country. Pairwise genetic differences, the low raggedness index, the form of the minimum-spanning network as well as the wide distribution of the most common haplotype supported the model of an expanding population. Hence, the results suggest that the Finnish capercaillie population is — or has been at least very recently — more or less continuous throughout the country.

Introduction

Habitat fragmentation almost always causes population size reduction and increased rate of loss of genetic variability. Today, increasing habitat fragmentation leading to population subdivision is an important concern in conservation efforts aiming to preserve genetic diversity. Discontinuous distributions of suitable or available habitats lead to a heterogeneous distribution of individuals of a species. This, in turn, promotes occurrence of inbreeding and genetic drift in local demes, with little or no gene flow between them. Behavioural factors, such as philopatry or short natal dispersal distances, can increase inbreeding and reduce genetic variation, and further depress the evolutionary potential of a species (Amos & Harwood 1998).

The capercaillie (*Tetrao urogallus*) inhabits late successional stages of Palearctic boreal conifer-dominated forests (taiga) from Scandinavia to eastern Siberia. In addition, it is patchily

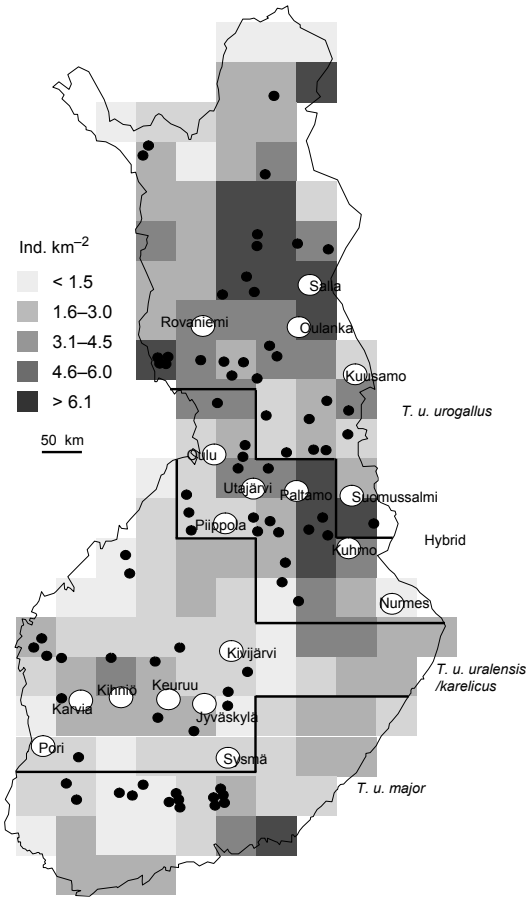

Fig. 1. Numbers of capercaillies (*Tetrao urogallus*) in Finland autumn 2003 according to the Finnish Game and Fisheries Research Institute. Single samples are marked with a black dot. White circles indicate population samples with ≥ 5 samples. Zonation is based on the subspecies distributions (Johansen 1957, Lindén & Teeri 1985).

distributed in central and western Europe following the distribution of coniferous forests, and the species is red-listed throughout this area (Storch 2000). The capercaillie is assumed to be highly sedentary (Storch 1995) and has a lek mating system, where a group of males display and females appear only for mating (Hjorth 1970). The optimal habitat is mosaic-like mixed forest, providing the capercaillie with suitable environment throughout the year (Helle *et al*. 1990, Storch 1995).

In Finland, the distribution of the capercaillie follows that of the Scots pine (*Pinus sylvestris*) from the southern coast to Lapland in the north. The species is absent only in the northernmost parts of the country and the highest densities can be found in Ostrobothnia and in southern and eastern Lapland (Fig. 1; Helle *et al*. 2002). Even though the distribution range is broad, it is also fragmented, and a metapopulation structure may exist, as in the Alps (Segelbacher & Storch 2002). Forests in southern Finland are fragmented to a higher degree than those in the northern parts of the country, and only small patches of suitable habitats, isolated from each other by human land use, exist (Kouki & Väänänen 2000). As the capercaillie is assumed a highly sedentary species, forest fragmentation caused by modern forestry can split up populations into small isolated sub-populations, which may exhibit less genetic variation, suffer from inbreeding and effects of genetic drift (Segelbacher *et al*. 2003).

Population decline of approximately 70% since the 1940s (Lindén & Rajala 1981) to ca. 750 000 birds (Väisänen *et al*. 1998: pp. 148–149) has most probably resulted from habitat loss and fragmentation, effective predation and hunting for adult birds (Helle *et al*. 1999). In 1964–1988 the proportion of female capercaillies decreased from 62% to 50% in southern Finland where the impact of human land use has been more severe. In contrast, in northern and eastern forest-dominated parts of the country the percentage of females remained at ca. 60% to 65% (Helle *et al*. 1999). The declining capercaillie populations are a general phenomenon in Europe (Storch 2000).

The human impact on the taiga habitats in Finland and NW Russia have differed after World War II. Small-scale forestry and agriculture have dominated in NW Russia, whereas in Finland both forestry and agriculture have been effective. In NE Finland and in NW Russia, large mature forest areas connected to the Oulanka National Park (Finland) and Paanajärvi National Park (Russia) still remain. These areas may maintain more genetic diversity because of a high density and a higher effective population size of the capercaillie.

The capercaillie population in Finland is assumed to represent three subspecies, namely *T. u. urogallus* in the northern, *T. u. uralensis* (also called *T. u. karelicus*) in the central and *T. u. major* in the southern parts of the country

(Johansen 1957, Lindén & Teeri 1985; Fig. 1). This division is based on several morphological characters (Johansen 1957, Koskimies 1958, Helminen 1963, Lindén & Väisänen 1986), differences in the lekking song structure (Jaakola 1999), and in some allozyme loci (Lindén & Teeri 1985). Additionally, a zone of a hybrid-between the subspecies *T. u. urogallus* and *T. u. uralensis* is assumed to exist across central Finland (Johansen 1957, Lindén & Teeri 1985; Fig. 1).

We investigated the genetic diversity of the capercaillie in Finland by analysing mitochondrial DNA (mtDNA) sequence variation. Until now, only five sequences for the capercaillie have been available in the GenBank; two identical sequences from Italy and Sweden (Lucchini *et al*. 2001), and three from Russia (Drovetski 2002). We asked the following three questions: (1) Has the recent fragmentation of old-growth forests in Finland caused such isolation between subpopulations of the capercaillie, which could result in local demes and genetic structuring? (2) Can the subspecies zones in Finland be detected with the aid of the mitochondrial DNA information? (3) Do the northern populations of the capercaillie exhibit more genetic variability than the populations in the other parts of the country?

Material and methods

Sampling of birds and laboratory methods

Capercaillie is listed in the Birds Directive (79/409/EEC) Article 7 (http://www.europa.eu.int/comm/environment/nature/legis.htm). However, the species referred to in Annex II/2 may be hunted in the EU Member States under certain regulations. According to this, the capercaillie is still legal game in Finland, even though it is classified as near-threatened (Rassi *et al*. 2001).

For this study we sampled altogether 302 capercaillies. Most of the sampled birds were a part of the normal game bag hunted during the legal hunting seasons 1995–2003. Tissue and feather samples were taken from the birds originally collected by hunters to be used for research at the Finnish Game and Fisheries Research Institute. Some samples were collected directly from found carcasses or moulted feathers. Sampling locations are presented in Fig. 1.

The feather quills were cut into small pieces and put into 100 µl buffer, which contained 0.1 M Tris-HCl (pH 8.5), 0.5 mM EDTA, 0.2% SDS, 0.2 M NaCl and 0.03 mg of Proteinase K. The quills were then incubated at 56 °C for three hours and afterwards centrifuged at 10 000 rpm for 10 min. After this, the DNA was precipitated from the supernatant with 200 µl of ice-cold ethanol and 10 µl of 3 M Na-acetate (pH 5.2), washed and diluted into 50 µl of deionized water. We extracted DNA from tissues using the standard phenol-chloroform method (Sambrook *et al*. 1989).

For the population analysis we PCR amplified the first 430 nucleotides of the mtDNA control region (downstream from the $tRNA^{Glu}$), i.e. the control region 1 (CR1), which is the most variable of the three domains of the CR in the capercaillie (Lucchini *et al*. 2001). CR1 was amplified with the forward primer LPPGLU (5´CACTGTTGTTCTCAACTACAGG), and the reverse primer H414 (5´GGTGTAGGGGGAAAGAATGGG) originally designed for the grey partridge *Perdix perdix* (Liukkonen-Anttila *et al*. 2002).

Amplification took place in 50 µl (containing 4 µl of DNA extract) using DyNazyme™ II DNA Polymerase (Finnzymes) for one cycle at 94 °C for 2 min, followed by 33 cycles at 94 °C for 1 min, 59 °C for 0.5 min and 72 °C for 1 min. The final extension at the end of the profile was 72 °C for 5 min. Negative controls were carried along the PCR reactions to detect contamination. Sequencing reactions were performed with the primer LPPGLU with Big Dye™ Terminator Cycle Sequencing Kit v. 3.0 (Perkin-Elmer) and run with ABI 377 automatic sequencer. Several unique samples were also sequenced with the reverse primer H414. Sequences have been deposited in GenBank (accession numbers AY580995–AY581047).

Sequence comparisons and statistical analysis

Sequence alignment was done both in Sequencher (v. 4.0.5, Gene Codes Corp.) and by eye in the

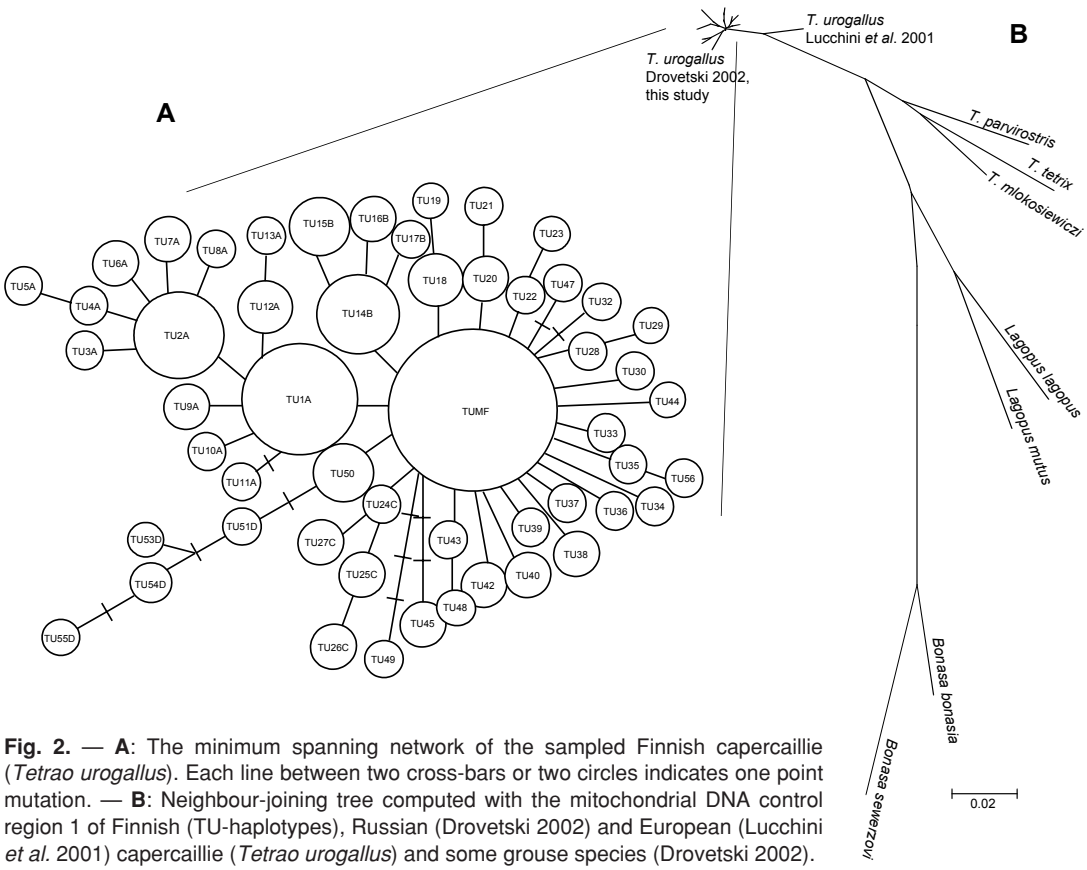

Fig. 2. — **A**: The minimum spanning network of the sampled Finnish capercaillie (*Tetrao urogallus*). Each line between two cross-bars or two circles indicates one point mutation. — **B**: Neighbour-joining tree computed with the mitochondrial DNA control region 1 of Finnish (TU-haplotypes), Russian (Drovetski 2002) and European (Lucchini *et al.* 2001) capercaillie (*Tetrao urogallus*) and some grouse species (Drovetski 2002).

BioEdit Sequence Alignment Editor (v. 5.0.9.). The first 19 nucleotides were ignored because of incompleteness in sequencing. The minimum-spanning network (Fig. 2A) was drawn manually based on the segregating sites (Appendix 1), Arlequin v. 2.0 (Schneider *et al.* 2000) and Treeview v. 1.6.6 (Page 2000).

The sequence data were divided into four zones, namely "urogallus" (n = 97), "hybrid" (n = 88) "uralensis" (n = 100), and "major" (n = 17) based on the distribution ranges of the suggested subspecies in Finland (Johansen 1957, Lindén & Teeri 1995; Fig. 1). The sequence data were also divided into 18 populations (Fig. 1). Birds within a range of 30 km were pooled together. This distance was adopted on the basis of the size of the home ranges of the capercaillie according to Storch (1997). Haplotypes found in each population are given in Appendix 2.

MEGA v. 2.1 (Kumar *et al.* 1993) was used to compute Tamura-Nei distances (Tamura & Nei 1993) between and within zones and for populations containing ≥ 10 samples. This model was chosen because of the low transversion–transition rate in the data. Nucleotide diversity (π; Nei 1987: eq. 10.5), haplotype diversity ($\hat{h}$; Nei 1987: eqs. 8.4 and 8.12), and Tajima's Ds (Tajima 1989) were calculated using DNAsp v. 3.51 (Rozas & Rozas 1999). We used the same programme to calculate the mismatch distributions and raggedness statistics (which quantifies the smoothness of the observed mismatch distributions and distinguishes between expanded and stationary populations) with coalescent simulations for the confidence intervals for raggedness index (r; Harpending 1994). Differences between diversity parameters were calculated with the Tukey-Kramer test (Box 9.11, Sokal & Rohlf 1995).

Haplotype frequencies, pairwise Φ_{ST}s (estimated using the haplotype frequencies assuming Tamura-Nei distances) and the analysis of

molecular variance (AMOVA; Excoffier *et al*. 1992) were calculated with Arlequin v. 2.00. The exact tests for differentiation (based on haplotype frequencies; Raymond & Rousset 1995) were carried out with the same programme.

Neighbour-joining tree including all Finnish, three Russian (Drovetski 2002) and one European (Lucchini *et al*. 2001) capercaillie haplotype sequences together with several other grouse species, was computed in MEGA v. 2.1 (Kumar *et al*. 1993) using Tamura-Nei distances and 1000 bootstraps to illustrate relationships between these taxa.

Results

Mitochondrial DNA control region 1 variation

The length of the whole mtDNA control region (CR) of the capercaillie is 1142 nucleotides (Lucchini *et al*. 2001), of which we sequenced the CR1 (430 nucleotides). The readable 411 nucleotides of the CR1 s equences exhibited 41 (10.0%) variable sites (22 transitions, 13 transversions, three one-bp and one three-bp indels). The low observed transition/transversion ratio is not very common in birds, but similar ratios are reported for several avian genera (Ruokonen & Kvist 2002). The mean nucleotide composition of the species in the CR1 — A 26.1%, T 28.3%, C 31.4% and G 14.2% — was similar to several other galliform species (Holder *et al*. 2000, Piertney *et al*. 2000, Liukkonen-Anttila *et al*. 2002). No heteroplasmy was found in the segregating sites and no background or double sequences were seen. Reverse sequencing did not reveal any false sequences.

Between-subspecies analysis

All Finnish haplotypes (Fig. 2A) were phylogenetically close to haplotypes found in birds from the Ural Mountains, Murmansk and Tver in Russia (Drovetski 2002; Fig. 2B), but clearly different from that found in the European birds (Italy and Sweden, Lucchini *et al*. 2001; Fig. 2B). The difference between the Finnish and the European haplotypes (3.3%) was of the same magnitude as the difference between the two mtDNA lineages of the grey partridge (3.6%), which are assumed to represent two different subspecies (Liukkonen-Anttila *et al*. 2002).

The most common haplotype (TUMF) was observed in 138 individuals (45.7% of all samples), whereas 52 haplotypes were identified in the remaining 164 individuals (Appendix 1). The TUMF haplotype dominated in three zones; 45 individuals were found in the "urogallus" zone, 48 in the "hybrid" zone and 39 individuals in the "uralensis" zone. Six TUMF individuals were also found in the "major" zone.

Tamura-Nei distances were of the same magnitude in each zone and among zones (Table 1). The highest (Tukey-Kramer: $p < 0.05$) nucleotide diversity (0.00437 ± 0.00047) was found in "urogallus", whereas the highest (Tukey-Kramer: $p < 0.05$) haplotype diversity was found in "major" (0.860 ± 0.055) (Table 2).

The minimum-spanning network (Fig. 2A) included a core of five haplotypes (TUMF, TU1A, TU2A, TU14B and TU50). All these haplotypes, together with haplotype TU18, were found in the zones "urogallus", "hybrid" and "uralensis". Five haplotypes were found solely in the "hybrid" zone (Appendix 1).

For the subspecies zones the analysis of molecular variance showed that 98.0% of the

Table 1. Mean (± SE) Tamura-Nei between-zone distances above diagonal, within-zone distances on the diagonal (in boldface), and mean net distances between zones below diagonal for the capercaillie (*Tetrao urogallus*) subspecies zones in Finland.

	n	"urogallus"	"hybrid"	"uralensis"	"major"
"urogallus"	97	**0.0044 ± 0.0013**	0.0037 ± 0.0011	0.0044 ± 0.0013	0.0044 ± 0.0014
"hybrid"	88	0.00003 ± 0.00002	**0.0029 ± 0.0011**	0.0036 ± 0.0013	0.0035 ± 0.0013
"uralensis"	100	0.00007 ± 0.00004	0.00005 ± 0.00003	**0.0043 ± 0.0015**	0.0041 ± 0.0015
"major"	17	0.00026 ± 0.00015	0.00014 ± 0.00010	0.00009 ± 0.00008	**0.0039 ± 0.0016**

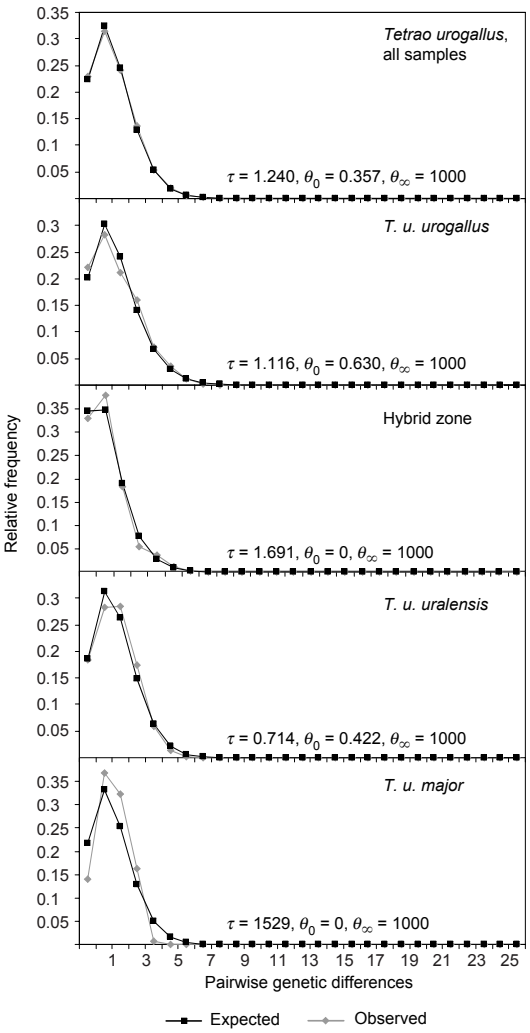

Fig. 3. The observed and expected mismatch distributions within the total population, three different subspecies and the hybrid zones of the Finnish capercaillie (*Tetrao urogallus*). Black lines indicate the expected and grey lines the observed values. Parameter τ refers to time in unit $0.5u$ generations, and u is the sum of per-nucleotide mutation rate in the DNA region under study (Rogers & Harpending 1992).

total variance was explained by the variation within zones (df = 298), and only 2.0% by the variation between zones (df = 3). According to the Φ_{ST}s, both "urogallus" and "hybrid" zones are differentiated from the "uralensis" and "major" zones. The exact tests of differentiation suggested that "urogallus" differed from "uralensis" and "hybrid" from "major" (Table 3).

All Finnish mtDNA control region 1 haplotypes grouped together with the sequences obtained from Russian capercaillies (Drovetski 2002). However, the sequence of European capercaillie (Lucchini *et al*. 2001) differed from our sequences clearly (3.3%) and was situated close to other grouse species in the neighbour-joining tree (Fig. 2B). The raggedness index for each zone is given in Table 2. The observed mismatch distribution followed the model of population expansion in every zone and also in the entire Finnish population (Fig. 3).

Between-populations analysis

In general, Tamura-Nei distances (Table 4) between populations were of the same magnitude than distances within populations. In Oulu, the within-population distance was quite low, because the population contained haplotypes closely related to each other. In contrast, the within-population distance in Jyväskylä was a bit higher than the average due to distinct haplotypes.

Nucleotide diversity was similar in the Kuusamo and central Finland populations, and no clear geographical pattern was seen in the diversity indices (Tukey-Kramer: $p < 0.05$; Table 5). When populations with fewer than 10 samples (Table 5) were included, it was clear that

Table 2. The sample size (n), nucleotide (π) and haplotype ($\hat{h}$) diversities, Tajima's D and its significance (p), and raggedness index (r) and its significance (p) for the capercaillie (*Tetrao urogallus*) subspecies zones in Finland. SD = standard deviation.

	n	π	SD	$\hat{h}$	SD	Tajima's D	p	r	p
"urogallus"	97	0.00437	0.00047	0.778	0.042	–1.96641	< 0.05	0.0212	0.12800
"hybrid"	88	0.00283	0.00039	0.670	0.053	–2.03994	< 0.05	0.0592	0.50000
"uralensis"	100	0.00421	0.00035	0.817	0.035	–1.62808	0.10 > p > 0.05	0.0378	0.28600
"major"	17	0.00380	0.00061	0.860	0.055	–0.46368	> 0.10	0.1040	0.32150
All	302	0.00389	0.00024	0.770	0.024	–2.14894	< 0.01		

populations in the north (Kuusamo, Rovaniemi, Salla and Oulanka) showed more variation (Tukey-Kramer: $p < 0.05$) than populations from the west coast (Oulu, Pori) or populations in the eastern parts of the country (Paltamo, Nurmes, Suomussalmi, Kuhmo). However, the sample sizes are too low to make any strong conclusions. All the populations included in the analysis shared two haplotypes, TUMF and TU1A, and haplotype TU2A was present in five of these populations.

When we focused on those seven populations containing 10 or more samples, variation within populations explained 99.5% (df = 126) of the total variance and only 0.5% (df = 6) was explained by the variation between populations. AMOVA showed, that these seven populations, namely Kuusamo, Oulu, Utajärvi, Karvia, Kihniö, Keuruu ja Jyväskylä did not differ from each other, and the Φ_{ST} values were low, in some cases negative (Table 6).

Discussion

Mitochondrial DNA variation in the capercaillie

One major haplotype (TUMF) occurred in 45% of all birds and it was common in every zone. We also found five additional common haplotypes. The northernmost zone "urogallus" was differentiated from the "uralensis" and "major" zones based on haplotype frequencies. This most probably resulted from the Kuusamo population, which was diverse and contained twelve different haplotypes. However, the TUMF haplotype was also found in this population. The "hybrid"

Table 3. Pairwise Φ_{ST}s (significant values in boldface) below diagonal and the significance of Exact tests of differentiation ($p < 0.05$, significant differences are indicated with '+') above the diagonal for the capercaillie (*Tetrao urogallus*) subspecies zones in Finland.

	"urogallus"	"hybrid"	"uralensis"	"major"
"urogallus"			+	+
"hybrid"	0.00536			+
"uralensis"	**0.01684**	**0.01317**		
"major"	**0.07617**	**0.08241**	0.03332	

Table 4. Mean (± SE) Tamura-Nei between-populations distances above diagonal, within-populations distances on the diagonal (in boldface) and mean net distances between populations below diagonal for seven capercaillie (*Tetrao urogallus*) populations in Finland.

	n	Kuusamo	Oulu	Utajärvi	Karvia	Kihniö	Keuruu	Jyväskylä
Kuusamo	30	**0.0047 ± 0.0013**	0.0038 ± 0.0012	0.0043 ± 0.0014	0.0046 ± 0.0015	0.0049 ± 0.0015	0.0048 ± 0.0015	0.0046 ± 0.0014
Oulu	14	0.00006 ± 0.00005	**0.0028 ± 0.0011**	0.0033 ± 0.0012	0.0036 ± 0.0014	0.0041 ± 0.0015	0.0039 ± 0.0013	0.0036 ± 0.0012
Utajärvi	27	0.00003 ± 0.00006	0.00000 ± 0.0000	**0.0039 ± 0.0015**	0.0041 ± 0.0015	0.0045 ± 0.0016	0.0043 ± 0.0014	0.0041 ± 0.0014
Karvia	10	0.00012 ± 0.00013	neg	neg	**0.0044 ± 0.0019**	0.0046 ± 0.0018	0.0045 ± 0.0016	0.0043 ± 0.0016
Kihniö	13	0.00004 ± 0.00008	0.00010 ± 0.00009	neg	neg	**0.0052 ± 0.0021**	0.0048 ± 0.0017	0.0046 ± 0.0017
Keuruu	16	0.00006 ± 0.00006	0.00008 ± 0.00016	neg	neg	neg	**0.0047 ± 0.0017**	0.0042 ± 0.0016
Jyväskylä	24	0.00010 ± 0.00009	neg	neg	neg	neg	neg	**0.0044 ± 0.0016**

zone was differentiated from the same two zones based on the haplotype frequencies. By using microsatellite markers, Segelbacher and Storch (2002) suggested that capercaillie populations in the Alps have a metapopulation structure with high levels of genetic variation and gene flow, but also some genetic differentiation between populations. This differentiation was, however, less pronounced than among central European isolated populations (Segelbacher *et al.* 2003). Conversely, our results indicate no metapopulation structure in Finland, but that Finnish capercaillie population is more or less continuous throughout the country in the light of mtDNA evidence.

Low nucleotide and high haplotype diversities found in each zone may indicate that the Finnish capercaillie population has experienced a bottleneck in the past and expanded rapidly thereafter. The haplotype composition of the Finnish capercaillie — one main haplotype, a few common haplotypes and several unique haplotypes — can also be seen in the microsatellite and mitochondrial single stranded conformational polymorphism (H. Mäki-Petäys *et al.* unpubl. data). Sudden expansion of a population leads to negative Tajima's *D* values well outside the neutrality range (Aris-Brosou & Excoffier 1996), and in the present study Tajima's *D* values for "urogallus" and "hybrid" zones were significantly negative. In addition, population expansion was supported by the mismatch distributions, the low raggedness index, the shape of the minimum-spanning network and the wide distribution of the most common haplotype.

When we compare the relationship between our sequences and those from Drovetski (2002) and Lucchini *et al.* (2001) with those obtained from *Anser* goose species and a numt sequence (Ruokonen *et al.* 2000), it is unlikely that we have sequenced a pseudogene in our study.

Table 5. The sample size (N), nucleotide (π) and haplotype ($\hat{h}$) diversities for capercaillie (*Tetrao urogallus*) populations and the total sampled population in Finland. SD = standard deviation.

Populations	n	π	SD	$\hat{h}$	SD
$n \geq 10$					
Kuusamo	30	0.00471	0.00087	0.749	0.084
Oulu	14	0.00279	0.00124	0.505	0.158
Utajärvi	27	0.00374	0.00076	0.783	0.072
Karvia	10	0.00431	0.00091	0.889	0.075
Kihniö	13	0.00510	0.00110	0.795	0.109
Keuruu	16	0.00468	0.00086	0.858	0.077
Jyväskylä	24	0.00430	0.00065	0.859	0.066
$n < 10$					
Salla	6	0.00547	0.00148	0.933	0.122
Oulanka	8	0.00569	0.00111	0.964	0.077
Rovaniemi	9	0.00470	0.00124	0.889	0.091
Piippola	6	0.00315	0.00079	0.867	0.129
Suomussalmi	7	0.00332	0.00139	0.583	0.183
Kuhmo	7	0.00190	0.00082	0.524	0.209
Paltamo	9	0.00290	0.00071	0.806	0.120
Nurmes	7	0.00142	0.00064	0.524	0.209
Kivijärvi	9	0.00235	0.00083	0.639	0.126
Sysmä	6	0.00332	0.00160	0.600	0.215
Pori	6	0.00299	0.00090	0.800	0.172
All	302	0.00389	0.00024	0.770	0.024

Female-mediated gene flow preserves variation?

The capercaillie is considered as a highly sedentary species. Males are reported to show high site fidelity (Storch 1995), whereas "multi-lek females" do exist (Storch 1997), and their home ranges may be several times larger than those of "single-lek females". During an annual cycle, capercaillie of one lek may inhabit an area of 30–50 km^2 (Storch 1995). Short dispersal combined with the high site fidelity of adult males has lead to prediction that isolation by distance allele frequencies should occur (Storch & Segelbacher 2000). However, "step-by-step" gene flow between populations may spread genes over longer distances than the dispersal ability of the species might predict. According to our results, gene flow between populations and subspecies zones could have effectively homogenised differences at the neutral mtDNA marker. In the capercaillie, females are assumed to be the dispersing sex (Koivisto 1963), and extensive female-mediated gene flow can have prevented mtDNA divergence, as it has been suggested to be the case in the red grouse *Lagopus lagopus scoticus* (Piertney *et al.* 2000). However, it is possible that the between-lek gene flow is higher than assumed earlier (H. Mäki-Petäys *et al.* unpubl. data) and has a strong impact on

maintaining a certain level of panmixia. Similar results on mtDNA were obtained from the Fennoscandian willow tit *Parus montanus*, another sedentary bird species associated with boreal coniferous forests (Kvist *et al*. 2001), and on microsatellites from the capercaillie in the Alps (Segelbacher & Storch 2002). Although haplotypes TUMF, TU1A, TU2A and TU14B were found in all four zones, it is more likely that this resulted from migration than that these haplotypes have evolved by parallel mutations. Flocking behaviour in the capercaillie was described by Koskimies (1957). Also unpublished observations from several hunters describe occasional mass movements of capercaillie, both males and females (J. Bisi & J. Heikkilä pers. comm.). However, it is possible that this pattern has resulted from past colonisation events.

A fragmentation period of 150 years (i.e. ca. 75 capercaillie generations), which covers the period of efficient forestry in Finland, seems insufficient for a genetic structure to evolve. However, mtDNA has its limitations in revealing recent population structuring and nuclear microsatellites should be used for this purpose. In short periods of time (tens of generations or fewer) problems in reproductive success inside forest fragments may arise (Kurki *et al*. 2000). They are connected to factors such as habitat quality, food availability and predation. Longer periods (tens to hundreds of generations) in fragmented populations may have genetic consequences due to genetic drift, mutations, and the absence of gene flow (Templeton *et al*. 1990, Brawn *et al*. 1996, Bates 2002). The forest fragmentation that has occurred in Finland appears to be too recent to be detected in the mtDNA structure of the capercaillie population, and no clear evidence of lower genetic diversity in southern Finland was found.

Subspecies question

Subspecies richness is reported to be high in sedentary species (Belliure *et al*. 2000). In this study we found no clear concordance between the subspecies' zones and the mtDNA variability. All four zones contained birds representing the most common haplotype and additionally three other haplotypes were shared among the zones. This may result from past colonisation processes, and these common haplotypes may have evolved before the present day population structure obtained its form. Unique haplotypes may have evolved later, but they may also represent vanishing haplotypes. If the subspecies exist, they may not be restricted to those geographical zones that have been presented by Johansen (1957) and Lindén and Teeri (1985).

Opposite results have been obtained in previous studies of genetic variation and the subspecies delimitation. Two lineages, western and eastern, that differ from each other by 14 nucleotides (3.6%) were found in the grey partridge in Europe (Liukkonen-Anttila *et al*. 2002), and their distribution was assumed to correspond to the distribution ranges of *Perdix perdix perdix* and *P. p. lucida*, respectively. Subspecies of rock ptarmigan *Lagopus muta* (Holder *et al*. 2000), wild turkey *Meleagris gallopavo* (Mock *et al*. 2002) and rock partridge *Alectoris graeca* (Randi *et al*. 2003) have distinct mitochondrial DNAs. The Pyrenean subspecies of the capercaillie *T. u. aquitanus* is distinctive from other European

Table 6. Pairwise Φ_{ST}s below the diagonal and the significance of Exact tests of differentiation ($p < 0.05$, significant differences are indicated with '+') above the diagonal for seven capercaillie (*Tetrao urogallus*) populations in Finland.

	Kuusamo	Oulu	Utajärvi	Karvia	Kihniö	Keuruu
Kuusamo				+		
Oulu	0.01142			+		
Utajärvi	0.00831	0.00416		+		
Karvia	0.01220	–0.01134	–0.00847			
Kihniö	0.01977	0.05065	0.01529	–0.03999		
Keuruu	0.00641	0.01904	–0.01714	–0.02836	–0.03947	
Jyväskylä	0.03035	–0.01387	0.00814	–0.04413	0.00287	0.01059

populations by microsatellites (Segelbacher *et al*. 2003). In contrast, morphological divisions and genetics do not concur, for example, in the sage grouse *Centrocercus urophasianus* (Benedict *et al*. 2003) or in the willow tit *Parus montanus* (Kvist *et al*. 2001). This may result from a recent divergence of the subspecies, present gene flow, or both. In the case of the capercaillie, the pattern most probably resulted from gene flow sufficient enough to homogenise the mtDNA genepool.

Variation between populations

For historical reasons, human impact on the taiga habitats in Finland and the NW Russia has been different. When a major forest landscape change occurred in Finland during the 1900s, and only some scattered patches of old-growth forests remained in eastern and southern Finland, on the Russian side of the border old and mature forests still covered large areas (Danilov *et al*. 1996, Kouki & Väänänen 2000, Lindén *et al*. 2000). This results in greater diversity of birds (Kouki & Väänänen 2000) and other wildlife (Danilov *et al*. 1996, Lindén *et al*. 2000) in Russian Karelia in comparison to Finland. Rare species and species of old-growth forests are more abundant in Karelia than in Finland. In fact, the taiga fauna in Fennoscandia is presumed dependent on the condition of the forests in Russia and on the connectivity across the border between Russia and Finland (Lindén *et al*. 2000). In the present study, we found the NE Finnish populations next to the Russian border (Kuusamo, Salla and Oulanka) to be genetically the most diverse ones. In Salla and Oulanka both nucleotide and haplotype diversities were high, and Kuusamo contained several unique haplotypes, which were closely related to each other and formed two separate clusters in the minimum-spanning network. Results of high genetic diversity in NE Finland have also been obtained in the Siberian tit *Parus cinctus* (Uimaniemi *et al*. 2003). This pattern may be an evidence of gene flow across the border from Russian Karelia, where the genetic diversity may be higher because of larger effective population size due to large suitable habitats. It is also possible that the large conservation areas in NE Finland and NW Russia have preserved high levels of genetic variation. However, no clear north–south cline could be detected in the diversity parameters. Furthermore, in northern parts of the country diversity values declined from east to west, but this was not the case in central parts of the country. Hence, the evidence supporting our hypothesis that the diversity should be higher in the areas close to the eastern border is weak at best.

Although the mitochondrial control region DNA did not reveal any clear effects of forest fragmentation on the genetic diversity of the capercaillie in Finland, some structuring could be seen based on haplotype frequencies. Gene flow may have been sufficient at least in the past, to maintain a state of panmixia in the Finnish capercaillie population. However, in the future we need more information about the contribution of the capercaillie males to the gene flow between populations and markers revealing more recent processes in Finnish capercaillie populations. This information is essential when planning the species conservation, hunting, and even forestry practices.

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Appendix 1. To the left capercaillie (*Tetrao urogallus*) mitochondrial DNA control region 1 haplotype names, their GenBank accession numbers, and the number of samples. In the middle the variable sites in mitochondrial control region 1. First nucleotide in the control region of the capercaillie is number one. First nineteen nucleotides are excluded due to sequencing ambiguities. Dash indicates a missing nucleotide, dot indicates similarity among sequences. Deviations from the main Finnish haplotype are indicated with the base name (A = adenine, T = thymine, C = cytosine and G = guanine). TUMF = main Finnish haplotype. To the right the numbers of different haplotypes found in each zone.

	1111 3344692555 5646144679	1122222222 7801111222 3302346259	2222222333 3456889000 5850049278	33333333334 02333344550 99023407340	urogallus	hybrid	uralensis	major
TUMF, AY580995 (138)	TGTTGACAGC	TTTCTCTATT	-TCGCGTCAC	ATC---GTATC	45	48	39	6
TU1A, AY580996 (34)	.....G....	....	....	....	11	13	9	1
TU2A, AY580997 (22)	.A...G....	....	....	....	6	5	10	1
TU3A, AY580998 (1)	.A...G....	....	..T.......	....	1			
TU4A, AY580999 (2)	.A...G....	....C.....	....	....			2	
TU5A, AY581000 (1)	.A...G....	...TC.....	....	....		1		
TU6A, AY581001 (2)	.A...G....	......C...	....	....			2	
TU7A, AY581002 (3)	.A...G....	....	.........T	....	3			
TU8A, AY581003 (1)	GA...G....	....	....	....	1			
TU9A, AY581004 (2)	.....G....	....C.....	....	....			2	
TU10A, AY581005 (1)	.....G....	....	....	..A.......		1		
TU11A, AY581006 (1)	.....GT...	....	..T.......	....			1	
TU12A, AY581007 (3)	..C..G....	....	....	....	1		2	
TU13A, AY581008 (1)	..C..G....	......C...	....	....			1	
TU14B, AY581009 (19)	....	......C...	....	....	1	6	8	4
TU15B, AY581010 (6)	....	......C...	...A......	....			5	1
TU16B, AY581011 (2)	....	C.....C...	....	....	1	1		
TU17B, AY581012 (1)	.........A	......C...	....	....	1			
TU18, AY581013 (4)	....	....	...A......	....	1	1	2	
TU19, AY581014 (2)	..C.......	....	...A......	....			2	
TU20, AY581015 (3)	....	....	..T.......	....		2	1	
TU21, AY581016 (1)	....	....	..T.......	.A........	1			
TU22, AY581017 (1)	....	.....A....	....	....		1		
TU23, AY581018 (1)	....	.....A....	....	......T....			1	
TU24C, AY581019 (1)	....	....	........T.	....	1			
TU25C, AY581020 (2)	..C.......	....	........T.	....	2			
TU26C, AY581021 (2)	..C.......	....	...A....T.	....			2	
TU27C, AY581022 (2)	...-......	....	........T.	....	2			
TU28, AY581023 (1)	......T...	....	....	....	1			

Continues

Appendix 1. Continued.

	1111 3344692555 5646144679	1122222222 7801111222 3302346259	2222222333 3456889000 5850049278	33333333334 02333344550 99023407340	urogallus	hybrid	uralensis	major
TU29, AY581024 (1)	......T..A	....	....	....	1			
TU30, AY581025 (1)	....	....	.C........	....		1		
TU32, AY581026 (1)	....	..CT......	....	....	1			
TU33, AY581027 (2)	....	....	C.........	....			2	
TU34, AY581028 (1)	..C.......	....	....	....	1			
TU35, AY581029 (1)	.A........	....	....	....			1	
TU36, AY581030 (1)	....	.C........	....	....			1	
TU37, AY581031 (1)	....	....	.......A..	....			1	
TU38, AY581032 (4)	....	.......G..	....	....	1	2	1	
TU39, AY581033 (1)	....	....	......C...	....	1			
TU40, AY581034 (4)	....	C	....	....			1	3
TU42, AY581035 (3)	....	....	....T.....	....	1	2		
TU43, AY581036 (1)	....-.....	....	....	....		1		
TU44, AY581037 (1)	....	....	....	.......G...			1	
TU45, AY581038 (2)	....	...TC.....	....	T.........	1	1		
TU47, AY581039 (1)	....	....	....	........TA.			1	
TU48, AY581040 (1)	....-G....	....	....	....	1			
TU49, AY581041 (1)	....	....	....	...TCG....G			1	
TU50, AY581042 (8)	....	........C.	....	....	5	2	1	
TU51D, AY581043 (1)	.......GA.	........C.	....	....	1			
TU53D, AY581044 (1)	.......GA.	....	.....A....	....	1			
TU54D, AY581045 (2)	.......GAA	....	....	....	2			
TU55D, AY581046 (1)	.A...G.GAA	....	....	....	1			
TU56, AY581047 (1)	.A........	....	...A......	....				1
				total	97	88	100	17

Appendix 2. Number of samples and found haplotypes in seven capercaillie (*Tetrao urogallus*) populations in Finland.

	Kuusamo	Oulu	Utajärvi	Karvia	Kihniö	Keuruu	Jyväskylä
TUMF, AY580995	15	10	11	2	5	6	9
TU1A, AY580996	4	1	5	2	2	2	1
TU2A, AY580997	2		3		2	2	2
TU4A, AY580999					1		1
TU5A, AY581000		1					
TU6A, AY581001				1			
TU8A, AY581003	1						
TU9A, AY581004						1	1
TU10A, AY581005			1				
TU11A, AY581006						1	
TU12A, AY581007	1					1	
TU13A, AY581008					1		
TU14B, AY581009			2				2
TU15B, AY581010				1	1	1	2
TU16B, AY581011		1					
TU18, AY581013				1			
TU19, AY581014							1
TU20, AY581015			1				1
TU23, AY581018						1	
TU26C, AY581021					1		
TU27C, AY581022	1						
TU30, AY581025			1				
TU33, AY581027				2			
TU34, AY581028	1						
TU35, AY581029							1
TU36, AY581030						1	
TU37, AY581031							1
TU38, AY581032	1		2				1
TU43, AY581036			1				
TU44, AY581037							1
TU50, AY581042		1		1			
TU51D, AY581043	1						
TU53D, AY581044	1						
TU54D, AY581045	1						
TU55D, AY581046	1						
n	30	14	27	10	13	16	24