Genetic evidence of capercaillie *Tetrao urogallus* dispersal sources and sinks in the Alps

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The aim of our study was to identify fine-scale genetic population structure of capercaillie *Tetra urogallus* populations in the Bavarian Alps, Germany. We studied five local populations and estimated genetic variation using 10 polymorphic microsatellite markers. We found no differences in the number of alleles per locus or the degree of heterozygosity between pairs of populations, but significant genetic variation among all populations. We detected significant genetic differentiation for pairs of populations separated by distances as short as 10 km. Genetically detected effective population sizes agreed with field data for relative population densities. Populations of peripheral study areas bordering the dairy-farming lowlands tended to show sink characteristics with immigration exceeding emigration. Our study confirmed that microsatellites have the potential to detect dispersal sources and sinks at a local scale and the results of studies like ours may help to develop improved, effective conservation plans for capercaillie.

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In landscapes altered by human activities, many species are restricted to small patches of habitat. Species that were once common have decreased both in distribution and density, and many have become extinct (Ceballos & Ehrlich 2002), mainly due to habitat deterioration, loss and fragmentation (Hilton-Taylor 2000). Previously contiguous populations have been turned into metapopulations (Hanski & Gilpin 1991), and connectivity by dispersal has become a key process for population dynamics and persistence. Metapopulation structure has recently been shown for capercaillie *Tetrao urogallus* in the Alps (Storch 1993, Storch & Segelbacher 2000, Segelbacher & Storch 2002). The birds occupy patches of mountain forests separated by open farmland valleys and interspersed by pastures, alpine vegetation and rocks above the treeline (Storch 2002a,b). Parallel to an ongoing population decline during the 20th century throughout Europe, the Alpine range of the capercaillie

has contracted (Storch 2001), and populations at the periphery are found to be more susceptible to decline and extinction than populations at the core of their range (Segelbacher & Storch 2002; P. Mollet, pers. comm., H. Zeiler, pers. comm.). We therefore hypothesise source-sink metapopulation characteristics for capercaillie in the Alps. Due to a generally poorer habitat structure (Storch 2002a,b) and a greater predation pressure in the vicinity of the farmland lowlands (I. Storch & E. Woitke, unpubl. data) populations at the edge of their range may function as sink populations, which are not self-sustaining but persist due to immigration. Mountain ranges surrounded by suitable capercaillie habitats, where extended farmland is absent and habitat structure is better, may serve as source populations and may thus be essential for the persistence of the metapopulation system (see Wiens 2001).
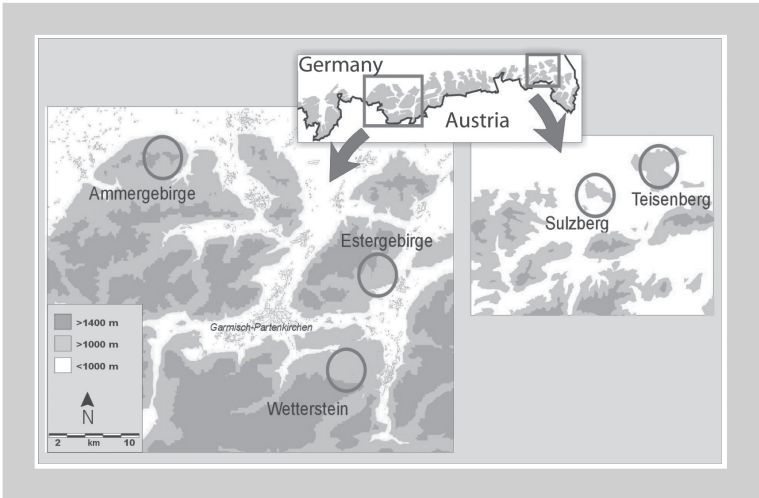

Figure 1. Location of the five study sites in the Bavarian Alps. Circles indicate the sampling areas. Areas between the altitudes of 1,000 and 1,400 m a.s.l. coincide with forests regularly used by capercaillie. Areas < 1,000 m a.s.l. are dominated by dairy farmland and settlements and areas > 1,400 m by pastures, alpine vegetation and rocks.

In this study, we aim to identify genetic evidence of source-sink dynamics among local capercaillie populations in the Bavarian Alps. For this purpose, we investigated metapopulation structure and gene flow of capercaillie from five separate mountain ranges using 10 highly polymorphic microsatellite markers. We expected populations at the edge of the range to show indications of a greater population decline (Segelbacher & Storch 2002) and specific characteristics of sink populations, such as low population size, high immigration and low emigration rates (Gaggiotti 1996).

Methods

Fieldwork

To investigate fine-scale population genetics of capercaillie, we sampled moulted feathers from two regions in the Bavarian Alps, Germany (Fig. 1), during the summers of 1997-2001. The western region consisted of the three adjacent mountain ranges Ammergebirge, Estergebirge and Wetterstein. The eastern region, which was separated from the western region by a distance of 110 km, consisted of the mountains Sulzberg and Teisenberg. Ammergebirge, Sulzberg and Teisenberg bordered the dairy-farming lowlands to the north of the Alps (see Fig. 1). The borderline coincided with the northern edge of the Alpine distribution of the capercaillie. The other ranges (Estergebirge, Wetterstein) were surrounded by forests inhabited by capercaillie on all sides. All study ranges were separated by 1-5 km wide farmland valleys. Capercaillie densities in the five ranges spanned from low (Ammergebirge) to high (Wetterstein) for the Bavarian Alps (Table 1). For the purpose of this paper, we use the term population for the birds in each of the mountain ranges studied, although they were clearly interconnected by gene flow and thus belonged to the same metapopulation system (Segelbacher & Storch 2002). We define dispersal sources and sinks exclusively with regard to the set of populations studied. Because we have no information on possible dispersers from or to other sites than those studied, we do not make any inferences regarding the demographic status of the populations.

For each range, data on relative capercaillie abundance and habitat suitability were available (see Table 1). In an earlier study (Storch 2002b), about 500 sample points regularly spaced at 200 m distances within an area of 2,000 ha had been established on each of the five mountains; at each sample point, habitat suitability for capercaillie had been assessed using a habitat suitability

Table 1. Standardised index of abundance and habitat suitability index (HSI) for five local capercaillie populations in the Bavarian Alps. Data from Storch 2002b and I. Storch, unpubl. data.

Population	Index of abundance	HSI
Ammergebirge	1.8	0.31
Estergebirge	6.4	0.46
Wetterstein	18.5	0.45
Sulzberg	2.8	0.25
Teisenberg	9.2	0.34

index (HSI) model, and incidence of indirect signs of capercaillie use, such as faeces and moulted feathers, had been recorded. The mean HSI score calculated over all sample points was used as an index of the suitability of the study areas as capercaillie habitat; the proportion of sample points with capercaillie signs was used as an index of capercaillie population abundance (see Storch 2002b for methods).

The feathers used in our study were collected in the 2,000-ha study areas (Storch 2002b). We obtained the following numbers of feather samples from males and females, respectively: 24 and 32 from Ammergebirge, 16 and 6 from Estergebirge, 52 and 12 from Wetterstein, 22 and 5 from Sulzberg and 58 and 42 from Teisenberg. For Ammergebirge we included four additional individuals from which feathers were found in the same forest, but not within the 2,000-ha study area, because we could not detect any significant genotypic or genic differences between these four extra individuals and those from within the 2,000-ha study area.

Genotyping

We extracted genomic DNA from all sampled feathers using the DNeasy Tissue Kit (Qiagen). Polymerase chain reaction (PCR) amplification and genotyping were conducted for 10 microsatellite loci as described in Segelbacher (2002a,b). Individuals were identified genetically to avoid multiple samples. All unique genotypes were used for the subsequent analysis, when at least seven loci could be typed per individual. As not all feathers could be genotyped due to DNA degradation (Segelbacher 2002a,b), the overall number of individuals analysed is smaller than the number of feathers sampled (see Table 2).

Statistical analysis

We estimated genetic variance within and among populations using genotype and allele frequencies of the microsatellite loci. We pooled samples for males and females, as we found similar results when analysing males separately. We used various computer programs for statistical analyses: Allele frequencies, observed and expected heterozygosity and mean number of loci were calculated using GENETIX version 4.02. Deviations from the Hardy-Weinberg equilibrium were tested using GENEPOP version 3.1d (Raymound & Rousset 1995) using a Markov chain method following the algorithm of Guo & Thompson (1992). Allelic richness (Petit, El Mousadik & Pons 1998) and F_{IS} were determined using FSTAT 2.93 (Goudet 2001). We assessed population differentiation by investigating the distribution of allele frequencies across populations using the log-

likelihood statistics G (Goudet, Raymond, Demeeus & Rousset 1996). We calculated genetic distances (D_{TL}; Tomiuk & Loeschcke 1991, 1995) using the program POPDIST, which is available at http://genetics.agrsci.dk/~bg/popgen. This measure is efficient in obtaining the correct phylogenetic topology of related populations and very robust against non-equilibrium conditions (Tomiuk, Gulbrandtsen & Loeschcke 1998).

We obtained pairwise F_{ST} estimates from GENEPOP 3.1d (Raymound & Rousset 1995, as per Weir & Cockerham 1984). To reduce the likelihood of Type I errors among multiple tests we applied a strict Bonferroni correction (Sokal & Rohlf 1995).

Based on coalescence theory, we calculated bi-directional gene flow (Nm) between pairs of populations and effective population size (N_e) by running MIGRATE (Beerli & Felsenstein 1999) 10 times and using the estimates of each run as starting values for the subsequent run. Unlike F_{ST}, MIGRATE accounts for directional gene flow and differences in sample size.

Estimates of the effective population size depend largely on the presumed underlying mutation rate. A mutation rate (i.e. the number of new mutations per locus per generation) of 5×10^{-4} is commonly accepted for microsatellites across a wide range of animal taxa (Ellegren, Lifjeld, Slagsvold & Primmer 1995). However, Primmer, Saino, Møller & Ellegren (1998) observed 44 mutations among 1,209 meioses in a tetranucleotide repeat of the barn swallow *Hirundo rustica*, which is equivalent to a mutation rate of 3.6×10^{-2}. Given the uncertainty about the true mutation rate, we calculated the effective population size N_e for both these mutation rates.

We furthermore estimated the number of immigrants and/or their descendants using the assignment test STRUCTURE (Pritchard, Stephens & Donelly 2000). This method uses a Gibbs sampler to implement a Bayesian clustering algorithm. Individuals were assigned probabilistically to one or more subpopulations based on their genotypes and the estimated allele frequencies per subpopulation. We used 10,000 iterations, following a burn-in period of 10,000 iterations, and the available prior population information.

Results

Genetic variability within populations
We found a high degree of genetic variation within all five populations, both in terms of average number of alleles and allelic richness per population. Furthermore, comparing observed and expected heterozygosity revealed that populations displayed high genetic diversity

Table 2. Genetic diversity of five local capercaillie populations in the Bavarian Alps. N gives the number of individuals analysed (number of males/females in brackets), A the mean number of alleles per locus, R the allelic richness, H_o the mean observed heterozygosity, H_e the expected heterozygosity and F_{IS}.

Population	N		A	R	H_o	H_e	F_{IS}
Ammergebirge	15	(9/6)	3.90	3.13	0.78	0.63	-0.21
Estergebirge	6	(5/-)	3.00	2.97	0.89	0.59	-0.42
Wetterstein	16	(13/3)	4.30	3.23	0.70	0.64	-0.07
Sulzberg	7	(7/-)	3.80	3.51	0.76	0.59	-0.21
Teisenberg	33	(19/14)	5.30	3.67	0.75	0.66	-0.11

(Table 2). The global probability test for Hardy-Weinberg equilibrium revealed that none of the populations deviated significantly from H-W equilibrium, after correcting for multiple comparisons. No pair of loci indicated significant departure from linkage disequilibrium.

Genetic variability among populations

We found significant genetic differentiation across all populations both within the western region (P < 0.002) and within in the eastern region (P < 0.004). The multilocus estimate of genetic differentiation was $F_{ST} = 0.059$ (P < 0.001) for the western region, indicating moderate genetic differentiation between populations separated by a maximum distance of 25 km. Pairwise F_{ST} estimates ranged within 0.015-0.071 (Table 3) and the degree of genetic differentiation between pairs of populations correlated with Tomiuk & Loeschcke's distance (D_{TL}). There were no significant genetic differences between the populations of Ammergebirge and Estergebirge. The populations of Sulzberg and Teisenberg in the eastern region were significantly different from each other according to the pairwise F_{ST} ($\theta = 0.03$, P < 0.05), but genetic differentiation was lower than in the western region, which was supported by Tomiuk & Loeschcke's distance ($D_{TL} = 0.082$).

Population size and gene flow

Based on the assumption of mutation-drift equilibrium and a mutation rate of 5×10^{-4}, effective population sizes were estimated to be five (Ammergebirge), 45 (Estergebirge), 680 (Wetterstein), 290 (Sulzberg) and 545 (Teisenberg) birds. However, when we adopted a mutation

Table 3. Pairwise F_{ST} (above diagonal) values and genetic distance (D_{TL}) for the three western population pairs (below diagonal). Figures in italics are significant after Bonferroni correction (P < 0.05).

Population	Ammergebirge	Estergebirge	Wetterstein
Ammergebirge	-	0.015	*0.067*
Estergebirge	0.094	-	*0.071*
Wetterstein	0.097	0.140	-

rate of 3.6×10^{-2}, effective populations of only 0.1 (Ammergebirge), 0.6 (Estergebirge), 9 (Wetterstein), 4 (Sulzberg) and 8 (Teisenberg) birds resulted. The latter estimate probably comes closer to the true order of magnitude. From field data we estimated the population of the Teisenberg Mountain Range to be 100-200 birds (Storch 1993; I. Storch, unpubl. data). When we assume a ratio of effective to estimated population size of 0.11 (after Frankham 1995), which is well in accordance with a range of other empirical studies (Frankham 1995, Galbusera, Lens, Schenck, Waiyaki & Matthysen 2000), 100-200 birds are equivalent to an estimated effective population size of 9-18 individuals. We conclude that the mutation rate of 3.6×10^{-2} is the more realistic model for the microsatellites in our capercaillie study.

Long-term, uni-directional migration rates (Nm) ranged between 0.0 and 13.2 (Table 4). Note, however, that Nm is a relative estimate that mainly reflects long-term gene flow and cannot directly be interpreted as N individuals per generation. Our results indicated immigration to but no emigration from Ammergebirge into the other study populations. In the Wetterstein population, emigration to Ammergebirge and Estergebirge clearly exceeded immigration from these two areas. Between the populations of Teisenberg and Sulzberg the gene flow seemed to be frequent.

We additionally applied an assignment test to identify migrants and to obtain an estimation of the current gene flow. Based on the Bayesian clustering method, all individuals clearly clustered to the population from which they had been sampled, and we could not identify any individual as an immigrant from one of the other populations in neither the western nor the eastern region. The test indicated that up to five generations ago no individual immigrated from another population.

Table 4. Uni-directional estimates of gene flow (Nm) between three capercaillie subpopulations in the western region and two in the eastern region as calculated using MIGRATE with 95% intervals (given in parentheses).

Western region		from	
Subpopulation	Ammergebirge	Estergebirge	Wetterstein
Ammergebirge	-	13.20 (11.43-15.20)	4.81 (3.51-6.51)
to Estergebirge	0.33 (0.19-0.51)	-	11.30 (10.18-12.69)
Wetterstein	0.00 (0.00-0.03)	7.54 (6.81-8.25)	-
Eastern group		from	
Subpopulation	Sulzberg	Teisenberg	
to Sulzberg	-	9.10 (8.22-10.08)	
Teisenberg	5.40 (4.81-6.03)	-	

Discussion

Genetic variability within and among populations

Our study clearly demonstrates the potential of DNA microsatellite markers to analyse local-scale genetic variation within and among capercaillie populations. However, microsatellite markers may or may not reflect the evolutionary potential and fitness of populations (Moss, Piertney & Palmer 2003), and any results should therefore be carefully interpreted. Local populations separated by as little as 10 km (see Fig. 1) exhibited significant genetic differentiation. However, between two of the five populations studied, Ammergebirge and Estergebirge, we did not detect any significant differentiation, although these study areas were separated geographically by approximately 20 km, including a 5-km wide, open farmland valley. Genetic homogeneity at the landscape level can be explained by demographic sinks that persist because of recurrent dispersal from a common source population (Gaggiotti 1996). The populations of Ammergebirge and Estergebirge both appear to be sustained by immigrants from the Wetterstein population, and this may explain why their genetic composition was quite similar. However, individuals might have immigrated from outside our study populations as well.

Apparently, genetic variation within populations of capercaillie has not been reduced by the present degree of spatial separation. The number of alleles and the degree of heterozygosity were consistently high in all investigated populations and none showed evidence of a bottleneck. As has been shown in pika *Ochonta princeps* (Peacock & Ray 2001), high levels of heterozygosity in a metapopulation can be explained by highly subdivided populations.

Previously, decreasing genetic differentiation was considered to be the major effect of habitat fragmentation and subsequent spatial separation of populations. More recently, some authors have suggested that in metapopulation systems, the overall genetic variation may be maintained due to genetic differentiation among local populations (Gaggiotti 1996, Harrison & Hastings 1996). Gaggiotti (1996) demonstrated that a collection of sinks could maintain a substantial proportion of the genetic variability observed in the source population. Despite their negative demographic effects, population sinks may thus help to maintain genetic diversity within metapopulations as they might serve as a temporary repository of genetic variation (Gaggiotti & Smouse 1996).

Population size and gene flow

We estimated dispersal between populations using two different procedures. F_{ST} and MIGRATE-based values mainly reflect long-term gene flow, whereas non-equilibrium assignment test reflect current dispersal events. We found high estimates, based on F_{ST} and MIGRATE-values, reflecting high ancestral rates of dispersal, but we could not detect any dispersers between the populations studied over the last five generations with the Bayesian clustering method (STRUCTURE). Failure to detect recent dispersal events between populations despite high rates of gene flow may have resulted from small sample sizes, and thus, is no proof of population isolation. However, an absence of observed dispersers may also reflect recent population fragmentation and decline (Galbusera et al. 2000).

Uni-directional gene flow estimates revealed uneven dispersal rates between the populations studied. In the western region, Ammergebirge at the edge of the Alpine capercaillie range, showed characteristics of a sink population. It did not produce emigrants and most likely consisted of the offspring of birds that immigrated from elsewhere. Sink populations are typically associated with inferior habitat quality relative to the sources (Dias 1996). Our field data (see Table 1) support this hypothesis, as both habitat suitability scores and capercaillie abundance were low in Ammergebirge. Also, according to genetic estimates, the Ammergebirge population had the lowest number of breeders. Estimates of effective population sizes (N_e) depend on the presumed underlaying mutation rate. We therefore adopted two different mutation rates for our data. Both mutation models, however, estimated the lowest effective population size for the Ammergebirge. Wetterstein, the study area with the highest capercaillie abundance and the largest number of potential breeders, functioned as a source population for both Ammergebirge and Estergebirge. The genetic data indicate that the Estergebirge population functioned as a stepping stone between Wetterstein and Ammergebirge, which is in congruence with its geographic location.

In the eastern region, we found a different pattern. Both populations were located at the edge of the Alpine range of the capercaillie and bordered the farming lowlands north of the Alps. Based on field studies, the capercaillie population in the 50-km² Teisenberg Mountain Range was estimated at 100-200 birds in the early 1990s (Storch 1993); repeated assessments of capercaillie abundance indicated that the population has increased through the years of our study (Storch 2002b; I. Storch, unpubl. data). On Sulzberg, capercaillie habitat suitability was poorer, and capercaillie abundance lower (see Table

1). Our study showed consistent gene flow between the two areas. This is supported by radio-tracking data, which had shown that four out of 40 adult capercaillie caught on Teisenberg migrated to Sulzberg on a seasonal basis (Storch 1993, 1995). Although we could genetically distinguish the Sulzberg from the Teisenberg birds, the results on effective population sizes indicated that the two local populations functioned as a single metapopulation unit.

Implications for conservation of capercaillie

Our study revealed that local capercaillie populations separated geographically by only 5-10 km showed significant genetic differentiation and subdivision. Our findings therefore suggest that a network of suitable habitat patches within the capercaillie's mean dispersal distance of about 5-10 km (see review in Storch & Segelbacher 2000) should be maintained in order to secure gene flow through highly fragmented capercaillie habitats such as the Alps. Gene flow among populations inhabiting spatially distinct habitat patches, however, depends greatly on population density and dynamics (e.g. Wiens 2001). Therefore, any given distance (within the dispersal ability of the species) between two neighbouring populations may or may not result in genetic differentiation. Between the populations of the mountain ranges Sulzberg and Teisenberg, separated by 5 km measured from edge to edge, we found high levels of gene flow, and radio-tagged birds were known to move between the two mountains. The estimated effective population size at Sulzberg was therefore high despite the fact that local abundance was low. Thus, at the time of our study, there was evidence of regular exchange between the two ranges, and Teisenberg functioned as the source for Sulzberg. As the number of emigrants is a function of population size (e.g. Ims & Hjermann 2001), however, a decline in the Teisenberg population, e.g. due to unfavourable changes in forestry practices, would lead to isolation and possibly extinction of the Sulzberg population, although the geographic distance between the two patches has remained the same.

Most likely, many of the small local capercaillie populations in the Bavarian Alps only persist due to their connectivity with other populations. Especially peripheral populations that border the extended farmland surrounding the Alps are most sensitive to population decline and extinction, because they may act as sinks: habitat quality, and thus breeding success is poor, and the population is maintained by dispersers from outside. Even where the habitat is favourable, however, source and sink functions may vary between years as a result of stochastic fluctuations in local rainfall patterns. Early

survival of capercaillie chicks strongly depends on weather conditions (e.g. Moss 1985). In the Bavarian Alps, the precipitation may vary greatly among neighbouring mountains (A. Zeitler, unpubl. data), and thus may cause uncorrelated fluctuations in local breeding success. Capercaillie conservation in the Alps should aim at securing productive source populations by maintaining high habitat suitability in the species' strongholds. In peripheral habitats that presently appear to function as population sinks, carrying capacity for capercaillie should be improved wherever possible, not only to increase local survival and reproduction, but also to help securing the entire metapopulation system. To achieve this goal, integration of capercaillie habitat needs into forest management plans is an urgent task that must be taken seriously by the responsible agencies.

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