

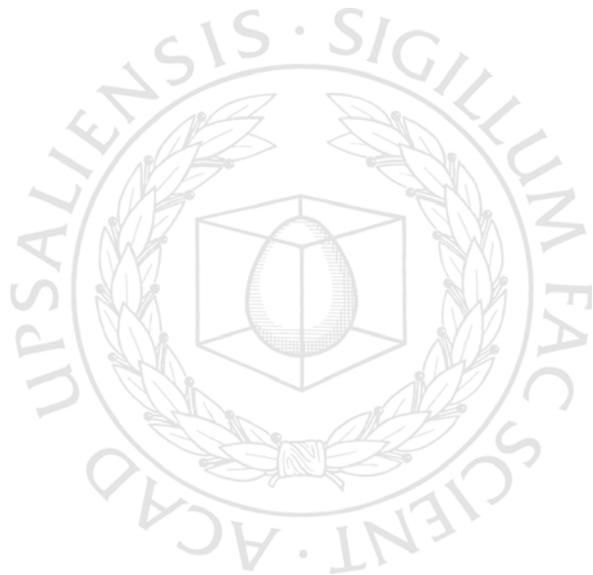


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Population Genetic Analyses of Natal Dispersal and Substructure in Three Bird Species

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ACTA
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2007

ISSN 1651-6214
ISBN 978-91-554-7045-6
urn:nbn:se:uu:diva-8339

Dissertation presented at Uppsala University to be publicly examined in Zootissalen, Evolutionary Biology Centre, Villavägen 9, Uppsala, Thursday, December 6, 2007 at 10:00 for the degree of Doctor of Philosophy. The examination will be conducted in English.

Abstract

Sahlman, T. 2007. Population Genetic Analyses of Natal Dispersal and Substructure in Three Bird Species. Acta Universitatis Upsaliensis. *Digital Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* 373. 33 pp. Uppsala. ISBN 978-91-554-7045-6.

Genetic variation within and among populations is a result of past and ongoing processes. Among the most important of such processes are dispersal, habitat fragmentation and selection. This thesis use neutral genetic variation as a tool to investigate these processes in three bird species.

In the Siberian jay, the timing of dispersal is dependent on social dominance among siblings. Mark-recapture data, radio-tracking and genetic variation was used to investigate whether timing of dispersal had an effect on dispersal distance. The results show that early dispersing individuals also disperse longer. In the same species, genetic correlation between neighbours was used to find areas with high production of philopatric individuals, which could be indicative of high habitat quality.

Great snipe populations in northern Europe have a breeding range divided into two regions. A Q_{ST} - F_{ST} approach was applied to study variation in selection between regions. Differentiation between the regions in neutral molecular markers was low, indicating high gene flow, or short time available for neutral divergence. Morphological divergence between the regions was high, and $Q_{ST} > F_{ST}$, which indicates divergent selection. Thus, neutral genetic markers can be misleading in identifying evolutionary significant units, and the Q_{ST} - F_{ST} approach might be valuable to identify targets for conservation.

Rock ptarmigan, or its ancestors, originated in Beringia, and spread throughout the Holarctic region. Their distribution has subsequently been affected by glaciations, most likely leading to withdrawals and re-colonisations. Neutral genetic variation among five populations around the northern Atlantic was investigated. There was strong genetic structure among the populations, and evidence that Scandinavian rock ptarmigan has been isolated from other populations for considerable time. Rock ptarmigan in Svalbard showed slightly lower genetic variation than others, and comparisons with other studies suggested an eastern colonisation route to Svalbard.

Keywords: Perisoreus infaustus, Gallinago media, Lagopus muta, relatedness, philopatry, biased dispersal, phylogeography, microsatellite, mitochondrial DNA

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ISSN 1651-6214

ISBN 978-91-554-7045-6

urn:nbn:se:uu:diva-8339 (<http://urn.kb.se/resolve?urn=urn:nbn:se:uu:diva-8339>)

List of papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

- I Sahlman T, Griesser M and Ekman J. Disentangling differential dispersal: demographics and genetics tell the same story in a group living species. Manuscript.
- II Sahlman T and Ekman J. Local genetic correlation reflects access to high quality habitat in a philopatric species, the Siberian jay. Manuscript.
- III Sæther SA, Fiske P, Kålås JA, Kuresoo A, Luigujõe L, Piirtney SB, Sahlman T and Höglund J. 2007. Inferring local adaptation from Q_{ST} – F_{ST} comparisons: neutral genetic and quantitative trait variation in European populations of great snipe. *Journal of Evolutionary Biology* 20, 1563–1576.
- IV Sahlman T, Segelbacher G and Höglund J. Phylogeography of rock ptarmigan in the north Atlantic area. Manuscript.

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Abbreviations

2D LSA

ESU

mtDNA

NSI

Two-dimensional local spatial auto-correlation

Evolutionary significant unit

Mitochondrial DNA

Nesting success index

Introduction

The genetic variation within species is a product of ongoing and past processes. These processes act both on various geographical and temporal scales and can result in genetic differentiation both within and between populations, and changes in genetic variation over time. Thus, current patterns of genetic variation can be used to make inferences about past and current events in the history of an organism.

Genetic processes

Mutation, i.e. any heritable change in the genetic material, is the ultimate source of genetic variation. Mutation rates are generally low, in the range of 10^{-8} to 10^{-9} mutations per nucleotide and generation in nuclear DNA, but vary between different types of genes (Frankham *et al.*, 2002). Mutations in coding regions that are not selectively neutral can give their bearers a fitness advantage or disadvantage relative to other individuals in the population, hence being eliminated or propagated (Hedrick, 1999, Frankham *et al.*, 2002). Most of the mutations that occur within coding regions are believed to be lethal or deleterious and hence eliminated by selection. The majority of mutations that occur outside coding regions are expected to be selectively neutral or nearly neutral.

Random genetic drift acts on selectively neutral or near-neutral alleles. Drift is an effect of random sampling of gametes that are drawn from one generation in the formation of next generation. Ultimately, drift leads to fixation of alleles and loss of genetic variation. The time to fixation is dependent on population size, and is longer in large populations than in small populations. Since drift is random, it leads to differences in allele frequencies between populations. The differentiating effect of drift can be counter-balanced by dispersal. Individuals that are born in one population but disperse to breed in another population potentially bring new alleles to the population where they breed (Hamilton and May, 1977). Random genetic drift and dispersal are the most important processes in determining variation between populations. Levels of dispersal can be affected both on large scales by barriers such as mountain ranges or oceans, and on small scales by natural or anthropogenic habitat fragmentation. In turn, dispersal affects a species ability to withstand effects of fragmentation such as loss of genetic variation through drift and inbreeding (Clobert *et al.*, 2001).

Variation in habitat among populations or along clines in continuous populations can cause different selection pressures in different geographic locations. If gene flow, i.e. dispersal, is sufficiently low in relation to the strength of selection, selection can give rise to local adaptations.

Glaciation and fragmentation

Climate has varied throughout the history of Earth, with glaciations and warmer periods following each other. The most recent glaciations, the Weichselian in Eurasia and the Wisconsin in North America, was an extremely large scale fragmentation event. The distributions of many species, e.g. oaks (*Quercus spp*) and brown bear (*Ursus arctos*, Taberlet *et al.*, 1998, Hewitt, 1999, and references therein), reindeer (*Rangifer tarandus*, Flagstad and Røed, 2003) and rock ptarmigan (*Lagopus muta*, Holder *et al.*, 1999), were subdivided or restricted to geographically confined refugia during the glaciation. In Europe, potential refugia were located on the Iberian Peninsula and south of the Alps (Taberlet *et al.*, 1998), and in North America potential refugia include Beringia, Banks Island and the areas south of the ice sheet (Dyke *et al.*, 2002). Following the warming of the climate and retraction of the ice cap, the distribution of species living in refugia expanded into new areas. If the expansion was quick enough, it could lead to loss of genetic variation, i.e. loss of alleles and decreased heterozygosity in colonised areas (Hewitt, 1999).

More recently, anthropogenic habitat fragmentation has had large impact on species distributions and abundance. In fact, fragmentation caused by human activities is the most important cause of species loss today (WCMC, 1992). Even when fragmentation does not cause extinction, it can reduce migration between populations and split viable populations into more vulnerable subpopulations.

Genetic markers

Different types of genetic markers are suitable to make inferences about processes within and between populations because of differences in mutation rates. Microsatellites are nuclear DNA elements consisting of repeated sequence motifs. They are thought to be selectively neutral or nearly so, and are biparentally inherited. A main mechanism of mutation for microsatellites is DNA replication slippage, whereby entire repeats are added to or eliminated from the new sequence copy. Therefore, microsatellites have relatively high mutation rates. This makes them ideal for studies of within population variation, or inferences about recent population events (Goldstein and Schlötterer, 1999).

Mitochondria are mostly maternally inherited organelles that occur in large numbers in vertebrate cells. Mitochondria contains DNA (mtDNA) organised in a circular double stranded molecule. The mtDNA do not undergo recombination and has a relatively high mutation rate, although not as

high as for microsatellite DNA. This type of marker has mostly been used to study population structure within species on larger geographical scales or further back in time than microsatellites (Awise, 2000).

Study species

In this thesis I have worked with three bird species, Siberian jay (*Persio-reus infaustus*), great snipe (*Gallinago media*) and rock ptarmigan (*Lagopus muta*) to study dispersal, local adaptation and genetic structure on small and large geographical scales.

Siberian jay (I, II)

The Siberian jay (*Perisoreus infaustus*) is a Corvid species that occurs in boreal forest from Norway in the west to north-east China in the east (Jons-son, 1992, Mackinnon and Phillipps, 2000). The species live on year-round territories in groups of 2-6 individuals. Groups can be multigenerational and consist of both relatives and non-relatives. (Ekman *et al.*, 1994, Ekman *et al.*, 2002). A single breeding attempt is made each year and in successful broods, 1 to 5 offspring fledge. About 40 % of fledglings (1 to 3 fledglings per brood) delay dispersal and remain on their natal territory for up to 3 years (Ekman *et al.*, 2001). Individuals that delay dispersal aggressively expel their subordinate siblings from the natal territory about 3-6 weeks after fledging. Subordinate siblings are thus forced to disperse. After dispersal they settle as immigrants in other territories rather than establishing new territories (Ekman *et al.*, 2002, Griesser *et al.*, submitted). Breeders are nepotistic towards their offspring that delay dispersal and provide them with benefits (e.g. predator protection and relaxed feeding conditions) that are withheld from immigrants to the group (Ekman *et al.*, 2000, Griesser, 2003, Griesser and Ekman, 2004, Griesser and Ekman, 2005, Nystrand, 2006). Delayed dispersers only inherit their natal territory if both parents die within short time. Instead they settle in territories neighbouring their natal territory, possibly to avoid inbreeding (Koenig and Haydock 2004).

Great snipe (III)

The great snipe (*Gallinago media*) is a migratory lekking shorebird species. Its breeding distribution ranges from the Scandinavian mountain range in the west, via Belarus, Poland and north-west Russia to the River Yenisei in the east. The habitat in the Scandinavian mountain range consists of mountain fens around the tree line (Kålås *et al.*, 1997), whereas the habitat in eastern Europe is dominated by lowland meadows subject to flooding in spring (Gromadzka *et al.*, 1985, Kuresoo and Leibak, 1994). Hence, habitat differences may predict different selection regimes in the two regions, whereas differences among populations within the regions are more likely to be af-

ected by genetic drift and migration alone. Until recently, great snipe was more common in lowland areas in Scandinavia and northern Europe. The species has declined in these areas, probably due to agricultural development during the recent 100-150 years. This decline has led to a disjunct breeding distribution, with a lack of breeding populations in lowland Scandinavia between the Scandinavian mountain range and the Baltic countries.

Rock ptarmigan (IV)

Rock ptarmigan (*Lagopus muta*) inhabits tundra and alpine regions throughout the northern hemisphere. The southern limit to its distribution includes the Pyrenees and the Alps in Europe, the mountain ranges in central Asia, the Japanese Alps, and the Aleutian Islands, Labrador and Newfoundland in North America. It is the only bird species where all populations inhabit tundra or alpine habitats through the whole life cycle. They are either resident year-round, or they withdraw from the most extreme conditions during winter (Løvenskiold, 1963, Holder and Montgomerie, 1993, Pedersen *et al.*, 2005). Natal and breeding dispersal distances or migration routes has not been studied in detail, although seasonal migration of up to 1000 km have been observed (Storch, 2000). Ringing of Svalbard rock ptarmigan (*L. m. hyperboreus*) showed that adults return to the same breeding sites between years, whereas juveniles never breed in the area where they were born (Unander and Steen, 1985). Analysis of grit in the crop of rock ptarmigan shot in Iceland indicated migration from Greenland to Iceland (Gudmundsson, 1972). The species is highly polytypic between populations, with up to 30 subspecies suggested (Storch, 2000).

Methods

Dispersal and fine-scale structure in Siberian jay (I, II)

We studied Siberian jays in a 65 km² area near Arvidsjaur in northern Sweden (65° 40' N 19° 0' E). The habitat in the study area is varied with forests ranging from young plantations of managed pine to unmanaged old-growth forests. The area is interspersed with natural openings like mires and small lakes, but also with clear-cuts.

The individuals in the studied population were marked with colour rings and numbered aluminium rings. We also collected a blood sample from each individual. To get information about breeding success in territories and natal territory of individuals, we ringed chicks before they left the nest or immediately thereafter. In cases where we did not manage to find the nest, we could determine the breeding success by assessing aggressive behaviour between adults and juveniles: adults are less aggressive towards their own offspring than towards other individuals (Ekman *et al.*, 1994, Griesser, 2003). All territories in the study area were visited on several occasions each year. Thus we could see where the ringed juveniles settled after natal dispersal.

In 2000 and 2003, all 33 juveniles hatched in 13 groups were equipped with radio-tags. With the help of the radio-tag we could follow early dispersers during their dispersal, and also find individuals that died. Since the radio-tags have a limited battery life, we could not follow delayed dispersers using this method.

We estimated dispersal distance from genetic data based on pairwise comparisons of genetic and geographic distance between individuals. Under isolation-by-distance (Wright, 1943), genetic distance increase linearly with the logarithm of geographic distance (Rousset, 2000). The slope of the regression of genetic distance on logarithm of geographic distance can be used to estimate natal dispersal distance, provided that the density of the population is known.

To assess the nesting success of territories relative to other territories, we calculated a nesting success index (NSI). The NSI of a single territory a single year is the difference between the actual reproductive success within the given territory (0 = failure, 1 = success) and the average nesting success in the whole population the same year. NSI was averaged over the years 2000-2003 and used to compare relative breeding success between territories.

To determine if differences in NSI was connected to fine-scale genetic structure, we investigated two-dimensional local spatial autocorrelation (2D LSA, Double *et al.*, 2005) between nearest neighbours. This analysis compares correlations in relatedness between nearest neighbours with relatedness correlations among all individuals. Thus, groups of neighbouring individuals that are more related to each other than the population average are detected.

Adaptive versus neutral variation in great snipe (III)

We studied morphology and neutral genetic variation in great snipe in five populations located in Norway, one in Poland and one in Estonia (Figure 1). We took morphological measures of tarsus, total head (bill plus head), bill (to end of skin), bill to nostril, maximum flattened wing length, and tail white (length of white field on outermost tail feather). We also collected blood samples from individuals in the studied populations.

Repeatability of measurements within individuals between years for tail white and wing length was used to estimate maximum heritability. We calculated pairwise F_{ST} between populations to assess neutral genetic differentiation, and pairwise Q_{ST} to assess differentiation in morphological traits. Under divergent directional selection, Q_{ST} is expected to be larger than F_{ST} , whereas if selection is favouring the same phenotype in different populations or regions, Q_{ST} is expected to be smaller than F_{ST} . If Q_{ST} and F_{ST} are roughly

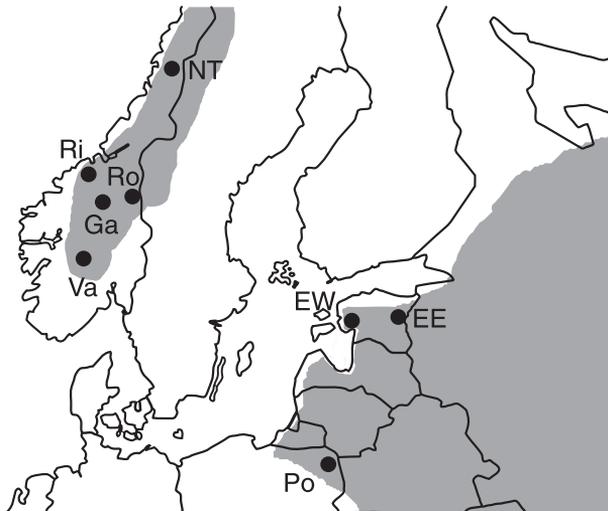


Figure 1. Great snipe populations in Norway (NT, Ri, Ro, Ga, Va) and eastern Europe (EW, EE, Po). Shaded areas indicate the breeding distribution.

equal, observed phenotypic differences between populations could be due to random genetic drift alone (Merilä and Crnokrak, 2001). We used partial matrix permutations of Q_{ST} and a matrix of type of comparison (within or between regions) controlling for neutral variation (F_{ST}), to determine whether Q_{ST} was larger between regions than within.

Phylogeography of rock ptarmigan (IV)

We obtained tissue or feather samples from rock ptarmigan in five populations: Svalbard, south-west Greenland, Iceland, Scandinavia and the Taimyr Peninsula (Figure 2). We sequenced the mtDNA control region and genotyped 12 microsatellite loci. We calculated genetic diversity within the populations, and genetic distances (Φ_{ST} and F_{ST}) between populations. To further assess indications of recent bottlenecks, we used the software Bottleneck (Cornuet and Luikart, 1996). Such indications include a heterozygosity excess due to alleles being lost more rapid than heterozygosity during a bottleneck event.

To put the genetic variation among our sampled populations in relation to other rock ptarmigan populations, we compared mtDNA sequences from



Figure 2. Sampled rock ptarmigan populations. The lighter grey area shows the minimum extent of arctic sea ice in summer (mean for years 2002-2005).

populations in this study to mtDNA sequences from other populations available online in Genbank.

Results and discussion

Natal dispersal in Siberian jay (I)

In our study of Siberian jays, 25 radio-tagged and untagged early dispersers were located after natal dispersal. These early dispersers had moved 6258 ± 1121 meters (mean \pm S.E.) on average, passing through 4.6 ± 0.8 territories before settling assuming a straight dispersal route. Radio-tagged dispersers were found farther away than untagged dispersers recovered within the study site (GLMM Poisson distribution, logarithm link: Wald statistic = 5.12, $p = 0.02$; year and territory as random variables; Table 1).

There were 130 confirmed delayed dispersers in the study population between 1990 and 2004. We managed to locate 71 of these after disappearance from the natal territory. Of these, 52 individuals had dispersed, whereas the remaining 19 individuals were found dead within the natal territory. The dead individuals had all been killed by predators. Delayed dispersers had moved on average 1325 ± 141 meters passing through 1.2 ± 0.10 territories. This is significantly shorter than early dispersers (Wald statistic = 6.07, $p = 0.002$; Table 1).

We genotyped adult individuals present in the study area during spring 2003 ($N = 114$) at ten microsatellite loci. The number of alleles varied between 3 and 15, and expected heterozygosity ranged between 0.09 and 0.90.

Table 1. Dispersal distances and estimated number of territories dispersers passed through before settling estimated from observational data and radio-tagged individuals. Distances are given as mean \pm standard error.

Category	N	Dispersal distance (meters)	No. territories passed through ¹
Radio tagged early dispersers	13 (3 ♂, 10 ♀)	8772 ± 167	6.4 ± 1.20
Untagged early dispersers found within study site	10 (3 ♂, 7 ♀)	2854 ± 81	2.2 ± 0.46
Untagged early dispersers found outside study site	2 (1 ♂, 1 ♀)	11150 ± 585	7.5 ± 4.50^2
All early dispersers	25 (7 ♂, 18 ♀)	6258 ± 1121	4.6 ± 0.78
All delayed dispersers	52 (31 ♂, 21 ♀)	1325 ± 141	1.2 ± 0.10
All dispersers	77 (38 ♂, 39 ♀)	2981 ± 453	2.4 ± 0.32

1. Assuming straight line dispersal.

2. Estimated number of territories only considering suitable habitat (excluding clear cuts, lakes and wetlands).

There was no evidence for deviance from Hardy-Weinberg equilibrium (Fisher's method for combining probabilities, d.f. = 20, $\chi^2 = 24.43$, $p = 0.22$).

There were on average 72 breeding individuals present in the population each breeding season from 2000 to 2004. The variance in number of offspring for these breeders was 1.486 for females (V_f) and 1.800 for males (V_m). Thus, we estimated the effective population size (N_e) to 79.04 individuals, and the effective population density (D_e) to 1.22 individuals/km².

For all birds analysed together, there was a negative correlation between kinship and log geographic distance, and a positive correlation between genetic distance and log geographic distance (regression slopes denoted blog_k and blog_a respectively; $\text{blog}_k = -0.007$, $p < 0.001$; $\text{blog}_a = 0.006$, $p = 0.01$), thus individuals were more related to each other on short distances compared to long distances (Figure 3). This is expected under isolation-by-distance. When delayed dispersers were analysed separately, the correlation slopes were steeper ($\text{blog}_k = -0.01669$, $p = 0.0211$; $\text{blog}_a = 0.0216$, $p = 0.0145$). There were no significant correlations when only early dispersers were analysed ($\text{blog}_k = -0.0017$, $p = 0.2624$; $\text{blog}_a = -0.0106$, $p = 0.0734$). The differences in regression slopes between all birds and delayed birds were statistically significant, as seen from the lack of overlap between 84 percent (equivalent to test on 5 % level, Payton *et al.*, 2003) confidence intervals (all birds: $-0.010 \leq \text{blog}_k \leq -0.002$, $-0.002 \leq \text{blog}_a \leq 0.012$; delayed birds: $-0.021 \leq \text{blog}_k \leq -0.013$, $0.014 \leq \text{blog}_a \leq 0.031$).

For all birds, neighbourhood size estimated from kinship was 172.6 (min = 114.9, max = 346.9), and from genetic distance 195.5 (min = 96.5, max = inf.). This gives estimates of average gene dispersal distance of 3.36 km (min = 2.74, max = 4.77) using kinship and 3.57 km (min = 2.51, max = inf) using genetic distance. For delayed dispersers, neighbourhood size was estimated to 55.7 (min = 47.8, max = 66.8) from kinship and 43.7 (min = 34.6, max = 59.2) from genetic distance. Average gene dispersal distance for delayed dispersers was estimated to 1.91 km (min = 1.76, max = 2.09) using kinship and 1.69 km (min = 1.50, max = 1.97) using genetic distance.

Both observational and genetic data support the conclusion that delayed dispersers stay closer to their natal territory than early dispersers after natal dispersal. In fact, most delayed dispersers do not relocate farther away than to a neighbouring territory. The average dispersal distances estimated from observational data and from genetic data corresponded to each other remarkably well, with overlapping distance estimates between observational data and at least one of the two genetic estimates for each category.

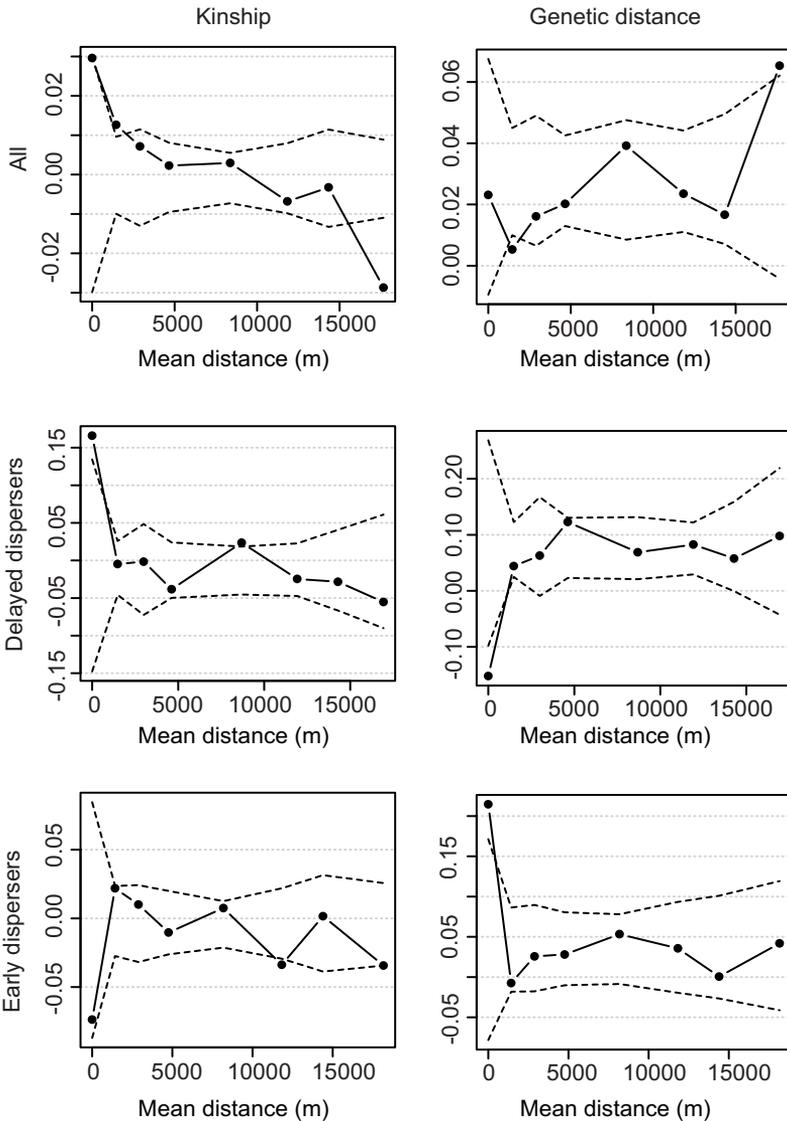


Figure 3. Average kinship coefficient (left hand graphs) and genetic distance (right hand graphs) for all individuals (top row), delayed dispersers (middle row) and early dispersers (bottom row). Mean geographic distance for eight distance classes. Dashed lines indicate the 95% confidence interval obtained by 10.000 permutations of spatial group locations among spatial groups.

Pure mark-recapture studies, where individuals are studied within a limited study area, often underestimate dispersal distances due to undetected long-distance dispersal events (Koenig *et al.*, 1996). We used both radio-tagging and genetic data to overcome such problems. Indeed, observational data for early dispersers show that radio-tracking has potentially provided less biased

estimates of the distance; estimates from radio-tagged individuals were significantly larger than estimates from individuals marked and recovered within the actual study area. However, the lack of genetic isolation-by-distance among early dispersers might suggest that the estimate is still slightly underbiased, calling for enlargement of the study area or inclusion of more populations to definitely settle the question about differential dispersal distances.

This study highlights the use of partitioning genetic data from individuals within the same population according to phenotypes to study differences in genetic structure and dispersal. This grouping might be according to different behavioural phenotypes, e.g. delayed and early dispersers in this study, or sex (Kummerli and Keller, *in press*, Double *et al.*, 2005), and can help elucidate whether dispersal is uniform across all individuals, or biased towards a subset of individuals. It would not have been possible to do the grouping according to behaviour without knowledge of each individual's dispersal history gathered over several years of study.

Local genetic correlation and habitat in Siberian jay (II)

We applied analysis of two-dimensional local spatial autocorrelation (2D LSA) to microsatellite data from 80 Siberian jay breeders present in the study area 2003. We found a heterogeneous pattern of relatedness between nearest neighbours across the study area: the breeders in 6 of 40 territories (Figure 4) were more related to their six nearest same-sex neighbours than to other individuals in the population (*lr*-values ranging between 0.17 and 0.20; *p*-values ranging between 0.01 and 0.04). Five of the indicated territories were from analyses of male breeders, and only one from analyses of female breeders. This suggests female-biased dispersal. A separate test for sex biased dispersal also indicated a trend towards female biased dispersal between the northern and the southern halves of the study area. Mean relatedness (Queller and Goodnight, 1989) was 0.04 among males (r_m) and -0.01 among females (r_f). The difference in relatedness between the sexes was only marginally significant (10000 permutations, alt. hypothesis $r_m > r_f$, $p = 0.07$). However, this method has the highest power of detecting dispersal bias when the dispersal ratio is high, around 80:20 (Goudet *et al.*, 2002).

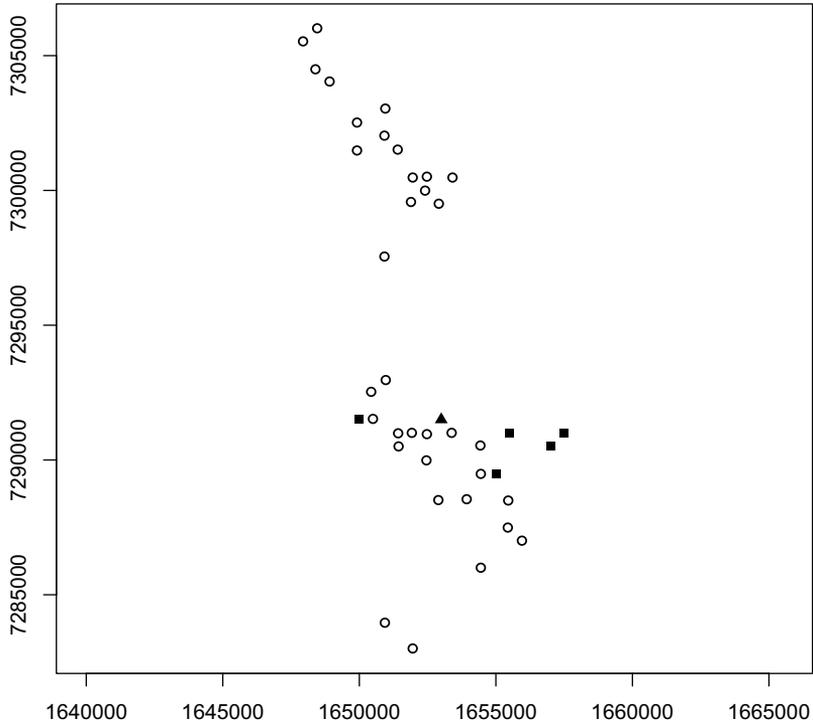


Figure 4. Territory positions in the study area. Open circles indicate occupied territories. Filled symbols indicate territories with high lr values, i.e. were males (squares) and females (triangle) were more related to their nearest same-sex neighbours than to other individuals. Axes are labelled with coordinates in meters, according to Swedish national grid (RT 90).

Nesting success index, a measure of relative breeding success, calculated for the years 2000 to 2003 was higher in territories with high lr values (median $NSI_1 = 0.28$) than in territories with average lr values (median $NSI_2 = 0.03$; Wilcoxon two-sample test, $n_1 = 6$, $n_2 = 31$, $W = 32.5$, $p < 0.01$). Although calculation of NSI for a set of territories does not separate intrinsic effects from the habitat of the territory from effects from the individuals living in the territory, earlier studies have shown a connection between habitat characteristics and NSI (Eggers *et al.*, 2005, Griesser *et al.*, 2006, Griesser *et al.*, 2007). Thus, this study points to a connection between habitat quality and local genetic autocorrelation and serves as a starting point for further analysis of fine-scale genetic structure.

Adaptive versus neutral variation in great snipe (III)

Neutral genetic variation among regions (eastern and western Europe) was weak and accounted for ca 2 % of the total genetic variation (Table 2). Most of the neutral genetic variation was accounted for within populations.

Annually re-grown traits (tail white and wing length) showed moderate to high repeatability within individuals between years, indicating substantial heritability. After correcting for measurement error repeatability estimates were of similar magnitude (~ 0.8) for both traits. Limiting analysis to adults increased the repeatability of wing length to 0.95.

There was large divergence among, but not within, regions for tarsus length and amount of tail white. A composite measure of bill length (PC1) showed only weak, however significant, divergence between populations (Table 3). There was no correlation between tarsus length and tail white within regions (east $r^2 = 0.001$, $n = 88$; west $r^2 < 0.001$, $n = 1416$). Partial matrix permutations of pairwise values showed that Q_{ST} for both tail white and tarsus length, but not for bill measures, were higher for comparisons between regions than for comparisons within regions. (Figure 5). Tail white and tarsus length showed much stronger divergence between regions ($Q_{ST} = 0.568$ and 0.416 respectively) than neutral genetic divergence ($F_{ST} = 0.018$, $R_{ST} = 0.051$). Divergence between regions in bill ($Q_{ST} = 0.01$) was lower than or similar to neutral genetic divergence.

Table 2. Hierarchical analysis of molecular variance (AMOVA) for eight great snipe populations categorised into two regions (Norway and Estonia/Poland) (a) based on weighed average R over five microsatellite loci, (b) based on microsatellite allele frequencies.

Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation	p -value	R_{ST}
(a)						
Among regions	1	51.72	0.263	2.41	0.053	0.024
Among populations within regions	6	51.81	-0.055	-0.5	0.46	-0.005
Within populations	332	3559.05	10.72	97.51		
Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation	p -value	F_{ST}
(b)						
Among regions	1	2.665	0.017	1.72	0.15	0.017
Among populations within regions	6	0.73	-0.023	-2.33	0.99	-0.023
Within populations	332	335.69	1.01	100.6		

Table 3. Nested ANOVAs of male morphological variation, and mean values in the eastern and western regions.

Trait	Source of variation	% of variation	d.f.	<i>p</i> -value	Eastern region Mean \pm SD (n)	Western region Mean \pm SD (n)
Tail white	Regions	48.04	1	<0.001	21.75 \pm 4.26 (88)	16.67 \pm 3.04 (1418)
	Populations within regions	1.38	6	0.083		
	Individuals	50.59	1498			
Tarsus	Regions	29.23	1	0.003	38.67 \pm 0.92 (88)	37.53 \pm 0.95 (1432)
	Populations within regions	3.70	6	0.011		
	Individuals	67.07	1512			
PC1	Regions	3.05	1	0.048	0.11 \pm 1.05 (87)	0.01 \pm 1.0 (1430)
	Populations within regions	-1.38	6	0.772		
	Individuals	98.33	1509			

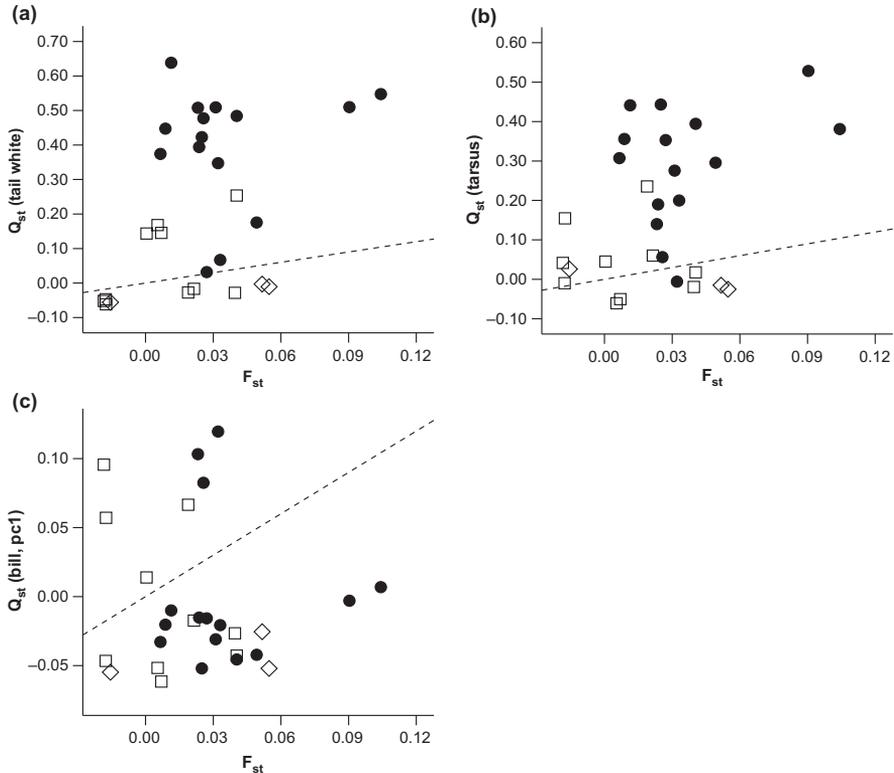


Figure 5. Population differentiation in quantitative traits (Q_{ST} , assuming $g = 1$ and $h^2 = 0.5$) in relation to neutral genetic differentiation (F_{ST}). For tail white (a) and tarsus (b), comparisons among populations in different regions (solid symbols) are larger than expected from the neutral differentiation whereas this is not the case for comparisons within the regions (open symbols, diamonds in east and squares in west). A different pattern is found for bill length (PC1) where Q_{ST} values among regions do not differ from within regions and are not larger than expected from neutral variation (c). Note the different scales on the Q_{ST} axes. Dashed lines are expectations if $Q_{ST} = F_{ST}$.

We recalculated Q_{ST} values for different assumptions about heritability (h^2) and magnitude of the additive genetic proportion of the between-population variance component (g). Conclusions drawn from comparisons of Q_{ST} and F_{ST} values were not sensitive to varying g and h^2 even outside realistic values.

Sampling of several populations within each region and controlling for neutral genetic variation among the same populations made it possible to avoid relying on specific assumptions about g and h^2 . Thus, this approach allows for robust conclusions about divergent selection among populations, even when common garden experiments are not feasible. However, it is

more difficult do draw conclusions about uniform stabilising selection. The weak divergence among regions in PC1 (bill length) corresponded to a pattern expected from neutral differentiation, or was possibly lower. Given the low values of neutral genetic population differentiation, it would be very hard to prove $Q_{ST} < F_{ST}$.

The general habitat of great snipe differs between the two regions. In the east, great snipe occur in sites that are subject to flooding early in the breeding season. This could have resulted in selection for longer legs than in the west, where great snipe occur on drier mountain sides. Furthermore, the amount of tail white has probably been under sexual selection (Höglund *et al.*, 1990, Saether *et al.*, 2000). Birds in the eastern region display at lower latitudes and earlier in the season (J. A. Kålås, S. A. Sæther, A. Kuresoo, L. Luigujõe, unpublished data), thus they perform their lekking display under considerably darker conditions than in the west.

This study has highlighted that neutral genetic differentiation is not sufficient to explain geographic differentiation in some quantitative traits in great snipe. Despite high gene flow there appears to exist local adaptation to different habitats. Thus this study highlights that although populations look similar regarding neutral genetic variation, selection could have caused local adaptations that might be important in a conservation context.

Phylogeography of rock ptarmigan (IV)

We studied genetic structure and variation in five populations of rock ptarmigan in the north Atlantic area. There was an overall tendency for lower genetic diversity in the Svalbard population (Table 4) that could indicate a smaller effective population size due to isolation. However, the bottleneck analysis did not pick up signs of recent population bottlenecks in any population.

Genetic structure among the studied populations was high: pairwise ϕ_{ST} from mtDNA varied between 0.41 and 0.98, and pairwise F_{ST} from microsatellite loci ranged between 0.09 and 0.29 (Table 5). We sequenced 1084 base

Table 4. Genetic diversity in four rock ptarmigan populations. Haplotype (h) and nucleotide (π) diversities are given with standard deviation. Allelic richness (AR) observed heterozygosity (H_o) and expected heterozygosity (H_e).

Population	h	π	AR	H_o	H_e
Greenland	0.704 \pm 0.058	0.00187 \pm 0.00019	4.35	0.61	0.67
Iceland	0.867 \pm 0.085	0.00209 \pm 0.00036	3.42	0.51	0.52
Svalbard	0.138 \pm 0.084	0.00013 \pm 0.00008	2.79	0.46	0.47
Scandinavia	0.524 \pm 0.209	0.00053 \pm 0.00024	4.07	0.69	0.66

Table 5. Pairwise genetic differentiation, F_{ST} below diagonal and ϕ_{ST} above diagonal. All values are significantly different from zero.

	Greenland	Iceland	Svalbard	Scandinavia
Greenland	-	0.43172	0.41208	0.84578
Iceland	0.09716	-	0.66689	0.87412
Svalbard	0.15952	0.28605	-	0.98102
Scandinavia	0.09082	0.24942	0.26645	-

pairs (bp) and found 16 different mtDNA haplotypes, but there was only one (haplotype L) that was shared between populations.

An unrooted network over haplotypes (Figure 6) showed that haplotype L was central to the network. Most other haplotypes differed by only one or two mutational steps from the central haplotype. However, haplotypes N, O and P differ from the more centrally located haplotypes by at least ten mutational steps. This difference was also supported in a minimum evolution phylogenetic tree, where haplotypes N, O and P clustered together, separately from all other haplotypes, in 76 % of 1000 bootstrap replicates (Figure 7). These haplotypes were only found in the Scandinavian population. This suggests that the Scandinavian population has been separated from other populations for a long period of time.

We aligned mtDNA sequences from this study with sequences from studies on Nearctic and Siberian populations (Holder *et al.*, 1999, Baba *et al.*, 2001, Lucchini *et al.*, 2001, Drovetski, 2002) to produce a 571 bp alignment. The alignment and an unrooted network (not shown here) showed that haplotype L most likely corresponds to a haplotype that is found across Siberia and Alaska, but not in the northern Canadian Arctic archipelago. Although

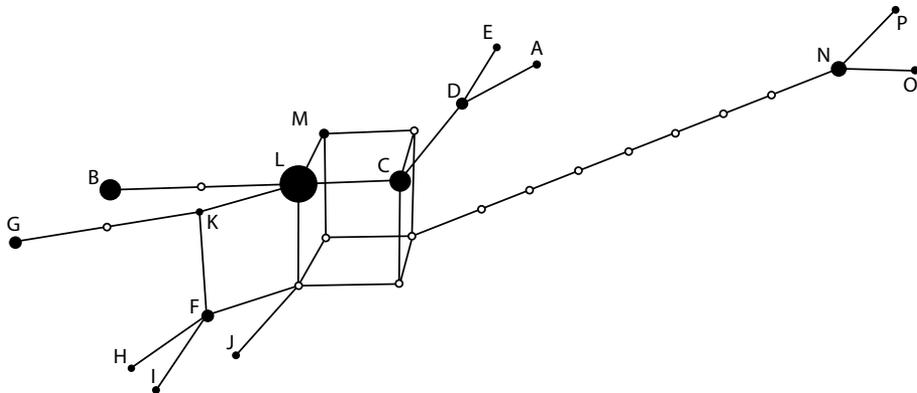


Figure 6. Unrooted network from the 16 mitochondrial control region haplotypes based on 1084 base pairs. Haplotype names (A-P) corresponds to Figure 7. Haplotype node sizes are proportional to haplotype frequencies. Unfilled nodes indicate inferred haplotypes not present within the sample. Each connecting line corresponds to one mutational step.

the phylogenetic analysis did not provide any conclusive evidence about the colonisation route to Svalbard for rock ptarmigan, this might point to an easterly route, from Siberia possibly via Franz Josef Land. The Svalbard subspecies (*L. m. hyperboreus*) is also present on Franz Josef Land (Løvenskiold, 1963).

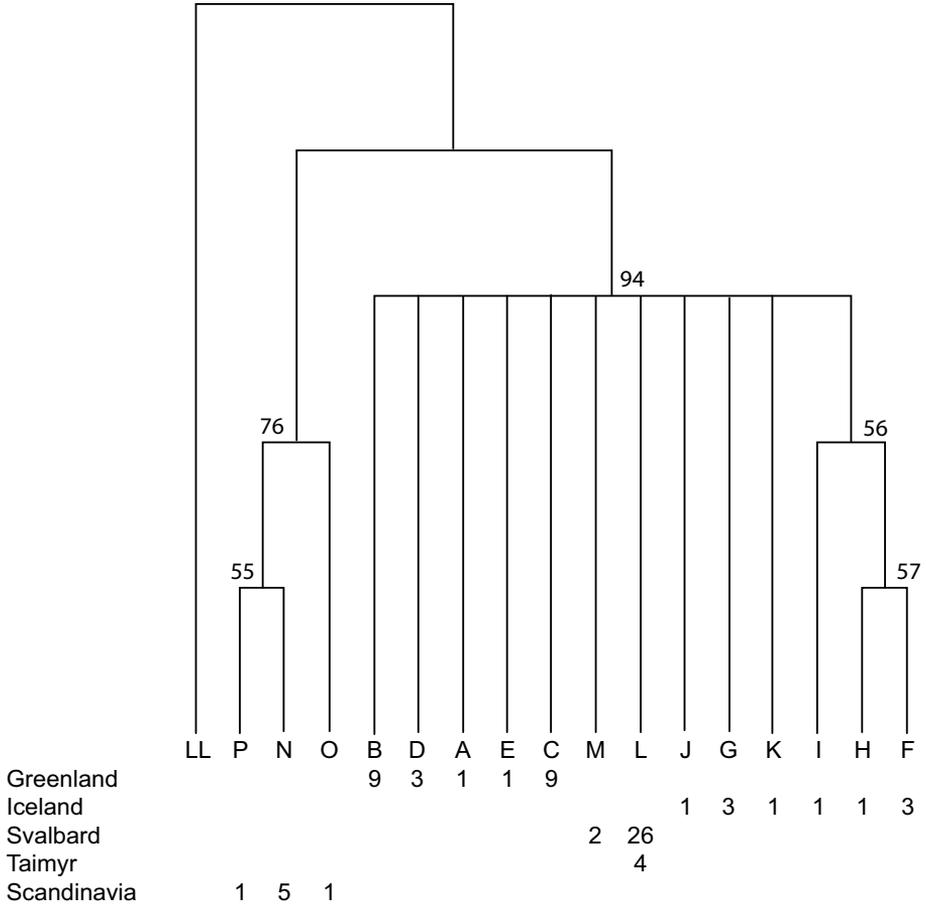


Figure 7. Minimum evolution phylogenetic tree showing all mitochondrial control region haplotypes (A-P). Bootstrap support values (percent of 1000 replicates) are shown on internal nodes. Nodes with bootstrap support less than 50 % are not shown. The tree is rooted through *Lagopus lagopus* (LL). The number of haplotypes found in five different populations is shown below the phylogenetic tree.

Conclusions

The results of this thesis has implications for conservation both directly for definition of evolutionary significant units (ESU) and exploration of genetic variation, and indirectly in providing a starting point to analyse fine-scale genetic patterns and the connection between habitat and population genetics.

The concept of ESUs has been proposed to account for the fact that there might be local adaptations within species. ESUs have often been defined on grounds of neutral genetic differentiation, although neutral differentiation might or might not be indicative of adaptive variation (Frankham *et al.*, 2002). This thesis demonstrates a case where neutral genetic differentiation would not indicate separate ESUs, although divergent selection leading to local adaptations might be present. Furthermore, a method to avoid assumptions and detect divergent selection in non-model species is proposed. We also demonstrate a case with high levels of neutral genetic differentiation, due to restricted gene flow.

Dispersal is an important factor in conservation: High dispersal rates between populations can replenish genetic variation that has been lost through genetic drift or population bottlenecks, and low rates can act in promoting local adaptation. Dispersal rates can be different between males and females, or between different behavioural categories. Knowledge of differential dispersal rates can be important to determine the target of conservation efforts. Genetic estimates of dispersal rates can often enhance the detection of long-distance dispersal events and can be an alternative to time-consuming and expensive observational studies for an estimate of overall dispersal distance and sex-biased dispersal rates. In this thesis we demonstrate a case where demographic and genetic data are used jointly to estimate differences in dispersal rates between categories of individuals. The results in this thesis also points to a genetic approach for detection of areas with high reproductive output which can be connected to habitat quality.

Sammanfattning (Summary in Swedish)

Den genetiska variationen hos en art är ett resultat av processer i såväl nutid som dåtid. Några av de viktigaste processerna som påverkar genetisk variation är migration, habitatfragmentering och selektion. I den här avhandlingen har jag använt mig av genetisk variation som ett verktyg för att studera de processerna.

Genetisk variation kan bara uppstå genom mutationer. Mutationshastigheten varierar mellan olika delar av ett genom, men är i regel låg. Den genomsnittliga mutationshastigheten är 1-10 mutationer per miljard baspar per generation. De flesta mutationer som uppstår i proteinkodande delar av genomet är skadliga eller dödliga och rensas snabbt bort genom selektion. En liten del av mutationerna som uppstår i kodande regioner har ingen effekt för reproduktionen eller överlevnaden hos bäraren, de är selektivt neutrala. Mutationer som uppstår utanför kodande regioner tros till största delen vara selektivt neutrala.

Det finns flera mekanismer, förutom selektion, som kan minska den genetiska variationen. En av de viktigaste är genetisk drift, som är resultatet av att endast en del av alla genetiska varianter som finns i en generation förs vidare till nästa. En genvariant som endast finns hos en liten del av individerna i en population försvinner ur populationen om ingen av bärarna fortplantar sig. Genetisk drift får större effekter i små populationer än i stora. Därför kan den genetiska variationen snabbt minska i en liten population som har isolerats från andra populationer inom samma art. Orsaken till isoleringen kan t.ex. vara fragmentering av habitat, eller (över ett lite längre tidsperspektiv) istäcket som under en istid tränger undan populationer till isfria områden. Minskningen av genetisk variation i isolerade populationer motverkas av migration. Då bryts isoleringen till viss del, och inflyttande individer har med sig "nya" genvarianter. Antalet inflyttande individer påverkas av det geografiska avståndet mellan populationer, och av om det finns några hinder på vägen mellan populationerna.

I de första två artiklarna har jag studerat spridning och genetisk variation i en population av lavskrika i norra Sverige. Unga lavskrikor lämnar sitt födelserevir vid olika ålder, beroende på hur dominant de är mot sina syskon. De mer dominant stannar i födelsereviret längre tid. I den första artikeln har jag använt data från ringmärkta och radiosändarmärkta lavskrikor tillsammans med data på genetisk variation för att ta reda på hur långt ungarna flyttar när de lämnar födelsereviret. Unga fåglar som flyttar tidigt flyttar också

längre, 6-7 km, jämfört med individer som flyttar senare, ca 2 km. Tidigare studier på lavskrika har visat att habitatkvalitet påverkar hur många ungar som föds i olika revir. I avhandlingens andra artikel jämförde jag graden av genetisk likhet mellan grannar, med graden av genetisk likhet i populationen i stort. I vissa områden var individerna mer lika sina närmsta grannar än slumpmässigt valda individer i populationen. I de områdena var också reproduktionsframgången, som är kopplad till habitatkvalitet, större. Det skulle alltså kunna vara möjligt att använda genetiska data för att få ledtrådar om områden som är viktiga för en populations överlevnad.

I den tredje artikeln jämförs morfologisk variation, i det här fallet variation i vinglängd, benlängd och näbblängd, med selektivt neutral genetisk variation mellan dubbelbeckasinpopulationer i Norge, Estland och Polen. Dubbelbeckasinens häckningsområde i norra Europa är delat i två delar, den skandinaviska fjällkedjan, och låglänta ängsmarker i Baltikum och Polen. Vi hittade stora skillnader i ving- och benlängd mellan de två regionerna, men nästan inga skillnader i neutral genetisk variation. Resultaten tyder på att populationerna i de bägge regionerna har utsatts för olika typer av selektion, trots att det inte finns några tecken på det när man studerar neutral genetisk variation. Inom naturvården har det varit vanligt att använda neutral genetisk variation som ett verktyg för att hitta ”unika” populationer. Om man också tar hänsyn till differentierande selektion så kan det bli lättare att hitta sådana populationer.

Slutligen, i den fjärde artikeln har genetisk variation hos fjällripor från fem olika populationer, Svalbard, Grönland, Island, Skandinavien och Tajmyr, studerats. Fjällripa förekommer på tundra och i alpina miljöer runt hela norra halvklotet. Arten, eller dess förfäder, härstammar från området runt Berings sund. Därifrån har de spridit sig österut mot resten av Nordamerika och Grönland, och västerut mot Sibirien och Europa. Efter den senaste istiden har fjällriporna koloniserat tidigare istäckta områden. Resultaten från studien visar att fjällripor i Skandinavien har varit isolerade från övriga populationer under lång tid, kanske sedan långt innan den senaste istiden. Fjällripor på Svalbard har en något lägre genetisk variation, vilket tyder på att ett begränsat antal individer har koloniserat Svalbard, eller att de har varit isolerade från andra populationer. Det går inte att med säkerhet säga varifrån fjällriporna koloniserade Svalbard, men genetiska likheter med ripor från Tajmyr tyder på att de kan ha kommit från Sibirien.

Acknowledgments

Loads of people have contributed in one way or another to this thesis.

MANY THANKS TO YOU ALL!!!

There are a couple of people I would like to mention. First I would like to thank my two supervisors, Jan Ekman and Jacob Höglund. Jan, thanks for opening the door to the world of Siberian jays already 15 years ago (remember?), and for giving me free rein to pursue almost anything I wanted, no matter if it was on this side of the world or down under. Jacob, thanks for always keeping the door open and being ready to chat about anything from fragment lengths to key fiddles, and for occasionally trying to tighten the rein. This thesis would not exist without the two of you!

Many people helped me in the lab over the years. Gunilla, thank you for running the lab, for teaching me the basics of genotyping, and especially for putting in a huge effort with the last samples for the ptarmigan paper. Peter, Ursula and Andreas, thanks for 102/108, 222/222, 135/147 and heaps of other genotypes. Kerstin, and earlier also Susanne, thank you for running “The Machine”!

Marianne, thank you for keeping the department, EBC and maybe even large parts of the world, running smoothly! Paperwork (not scientific papers), has been a breeze thanks to you.

A big Thank You to all the co-authors of the papers in this thesis. Thanks for your knowledge and skills!

Kalle, thanks for being a splendid roommate. I think that you think that I think you disturbed me. You didn't! It's been a pleasure, and what would life be without music, a good armchair and an aquarium.

Magdalena, thanks for having good views on essentials, and funny views (“Would you rather...?”) on other stuff. Bea, you were one week ahead of me and already knew all the answers, which made my life a lot simpler these last few weeks. And thanks for cheering me on!

To *all* other people at PopBio, past and present: thanks for making PopBio such a good place to be for work, discussions, coffee drinking, partying...

Life is not only work and research, and it would be quite meaningless without friends. Thank you for your support, fun times and shared memories! I'll be back, now...

My family has encouraged and supported me from the start, whatever whim I wanted to follow. Thanks for being there all the time! (By “start” I

mean the lizard Efraim who lived in a sandy landscape, created by me, in a bucket. It must have been in the late 70's.)

Tanja, thanks for believing in me and cheering me on when I needed it. *You* are the best part of my life!

This thesis was funded by FORMAS, Naturvårdsverket and Vetenskapsrådet (to J.E.); by Naturvårdsverket and Vetenskapsrådet (to J.H.); and by C.F. Liljewalchs resestipendium, H. Nyqvists testamentsfond, Stiftelsen för Zoologisk forskning and Stiftelsen Lars Hiertas minne (to T.S.).

References

- Avice, J. C. (2000) *Phylogeography: the history and formation of species*, Harvard University Press.
- Baba, Y., Fujimaki, Y., Yoshii, R. & Koike, H. (2001) Genetic variability in the mitochondrial control region of the Japanese Rock Ptarmigan *Lagopus mutus japonicus*. *Japanese Journal of Ornithology*, 50, 53-64.
- Clobert, J., Danchin, E., Dhondt, A. A. & Nichols, J. D. (Eds.) (2001) *Dispersal*, Oxford, Oxford University Press.
- Cornuet, J. M. & Luikart, G. (1996) Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. *Genetics*, 144, 2001-2014.
- Double, M. C., Peakall, R., Beck, N. R. & Cockburn, A. (2005) Dispersal, philopatry, and infidelity: Dissecting local genetic structure in superb fairy-wrens (*Malurus cyaneus*). *Evolution*, 59, 625-635.
- Drovetski, S. V. (2002) Molecular phylogeny of grouse: individual and combined performance of W-linked, autosomal and mitochondrial loci. *Systematic Biology*, 51, 930-945.
- Dyke, A. S., Andrews, J. T., Clark, P. U., England, J. H., Miller, G. H., Shaw, J. & Veillette, J. J. (2002) The Laurentide and Innuitian ice sheets during the Last Glacial Maximum. *Quaternary Science Reviews*, 21, 9-31.
- Eggers, S., Griesser, M. & Ekman, J. (2005) Predator-induced plasticity in nest visitation rates in the Siberian jay (*Perisoreus infaustus*). *Behav. Ecol.*, 16, 309-315.
- Ekman, J., Bylin, A. & Tegelström, H. (2000) Parental nepotism enhances survival of retained offspring in the Siberian jay. *Behavioral Ecology*, 11, 416-420.
- Ekman, J., Eggers, S. & Griesser, M. (2002) Fighting to stay: the role of sibling rivalry for delayed dispersal. *Animal Behaviour*, 64, 453-459.
- Ekman, J., Eggers, S., Griesser, M. & Tegelström, H. (2001) Queuing for preferred territories: Delayed dispersal of Siberian jays. *Journal of Animal Ecology*, 70, 317-324.
- Ekman, J., Sklepkovych, B. & Tegelström, H. (1994) Offspring retention in the Siberian jay (*Perisoreus infaustus*): The prolonged brood care hypothesis. *Behavioral Ecology*, 5, 245-253.
- Flagstad, O. & Røed, K. H. (2003) Refugial origins of reindeer (*Rangifer tarandus* L.) inferred from mitochondrial DNA sequences. *Evolution*, 57, 658-670.
- Frankham, R., Ballou, J. D. & Briscoe, D. A. (2002) *Introduction to conservation genetics*, Cambridge University Press.
- Goldstein, D. B. & Schlötterer, C. (Eds.) (1999) *Microsatellites: evolution and applications*, Oxford, Oxford University Press.
- Goudet, J., Perrin, N. & Waser, P. (2002) Tests for sex-biased dispersal using biparentally inherited genetic markers. *Molecular Ecology*, 11, 1103-1114.
- Griesser, M. (2003) Nepotistic vigilance behavior in Siberian jay parents. *Behavioral Ecology*, 14, 246-250.

- Griesser, M. & Ekman, J. (2004) Nepotistic alarm calling in the Siberian jay, *Perisoreus infaustus*. *Animal Behaviour*, 67, 933-939.
- Griesser, M. & Ekman, J. (2005) Nepotistic mobbing behaviour in the Siberian jay, *Perisoreus infaustus*. *Animal Behaviour*, 69, 345-352.
- Griesser, M., Nystrand, M., Eggers, S. & Ekman, J. (2007) Impact of Forestry Practices on Fitness Correlates and Population Productivity in an Open-Nesting Bird Species. *Conservation Biology*, 21, 767-774.
- Griesser, M., Nystrand, M. & Ekman, J. (2006) Reduced mortality selects for family cohesion in a social species. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, 273, 1881-1886.
- Gromadzka, J., Stawarczyk, T. & Tomialoje, L. (1985) Breeding waders in Poland. *Wader Study Group Bulletin*, 43, 29-33.
- Gudmundsson, F. (1972) Grit as an indicator of the overseas origin of certain birds occurring in Iceland. *Ibis*, 114, 582.
- Hamilton, W. D. & May, R. M. (1977) Dispersal in stable habitats. *Nature*, 269, 578-581.
- Hedrick, P. W. (1999) *Genetics of populations*, Jones and Bartlett Publishers.
- Hewitt, G. M. (1999) Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society*, 68, 87-112.
- Holder, K. & Montgomerie, R. (1993) Rock ptarmigan (*Lagopus mutus*). In: Poole, A. & Gill, F. (Eds.) *The birds of North America*. American Ornithologists' Union.
- Holder, K., Montgomerie, R. & Friesen, V. L. (1999) A test of the glacial refugium hypothesis using patterns of mitochondrial and nuclear DNA sequence variation in rock ptarmigan (*Lagopus mutus*). *Evolution*, 53, 1936-1950.
- Höglund, J., Eriksson, M. & Lindell, L. E. (1990) Females of the Lek-Breeding Great Snipe, *Gallinago-Media*, Prefer Males with White Tails. *Animal Behaviour*, 40, 23-32.
- Jonsson, L. (1992) Fåglar i Europa med Nordafrika och Mellanöstern, Wahlström & Widstrand.
- Koenig, W. D., Van Vuren, D. & Hooge, P. N. (1996) Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends in Ecology & Evolution*, 11, 514-517.
- Kummerli, R. & Keller, L. (in press) Contrasting population genetic structure for workers and queens in the putatively unicolonial ant *Formica exsecta*. *Molecular Ecology*, OnlineEarly access.
- Kuresoo, A. & Leibak, E. (1994) Breeding status of snipes in Estonia and in the eastern Baltic region. IN Kalchreuter, H. (Ed.) *Fourth European Woodcock and Snipe Workshop*. Slimbridge, Gloucester, UK, IWRP.
- Kålås, J. A., Fiske, P. & Höglund, J. (1997) Food supply and breeding occurrences: The West European population of the lekking great snipe *Gallinago media* (Latham, 1787) (Aves). *Journal of Biogeography*, 24, 213-221.
- Lucchini, V., Höglund, J., Klaus, S., Swenson, J. & Randi, E. (2001) Historical biogeography and a mitochondrial DNA phylogeny of grouse and ptarmigan. *Molecular Phylogenetics and Evolution*, 20, 149-162.
- Lövenskiöld, H. L. (1963) *Avifauna Svalbardensis*, with a discussion on the geographical distribution of the birds in Spitsbergen and adjacent islands, Norsk Polarinstitut.
- Mackinnon, J. & Phillipps, K. (2000) *A field guide to the birds of China*, Oxford University Press.
- Merilä, J. & Crnokrak, P. (2001) Comparison of genetic differentiation at marker loci and quantitative traits. *Journal of Evolutionary Biology*, 14, 892-903.

- Nystrand, M. (2006) Influence of age, kinship, and large-scale habitat quality on local foraging choices of Siberian jays. *Behav. Ecol.*, 17, 503-509.
- Payton, M. E., Greenstone, M. H. & Schenker, N. (2003) Overlapping confidence intervals or standard error intervals: what do they mean in terms of statistical significance? *Journal of Insect Science (Online)*, 3, 34.
- Pedersen, Å. Ø., Overrein, Ø., Unander, S. & Fuglei, E. (2005) Svalbard Rock ptarmigan (*Lagopus mutus hyperboreus*) - a status report. Rapportserie. Tromsø, Norwegian Polar Institute.
- Queller, D. C. & Goodnight, K. F. (1989) Estimating Relatedness Using Genetic Markers. *Evolution*, 43, 258-275.
- Rousset, F. (2000) Genetic differentiation between individuals. *Journal Of Evolutionary Biology*, 13, 58-62.
- Saether, S. A., Fiske, P., Kalas, J. A. & Gjøl, J. M. (2000) Females of the lekking great snipe do not prefer males with whiter tails. *Animal Behaviour*, 59, 273-280.
- Storch, I. (2000) Status Survey and Conservation Action Plan 2000-2004: Grouse. IUCN, Gland, Switzerland, and The World Pheasant Association, Reading, UK.
- Taberlet, P., Fumagalli, L., Wust-Saucy, A. G. & Cosson, J. F. (1998) Comparative phylogeography and postglacial colonization routes in Europe. *Molecular Ecology*, 7, 453-464.
- Unander, S. & Steen, J. B. (1985) Behavior and social structure in Svalbard rock ptarmigan (*Lagopus mutus hyperboreus*). *Ornis Scandinavica*, 16, 198-204.
- WCMC (1992) Global biodiversity: status of the world's living resources, Chapman and Hall.
- Wright, S. (1943) Isolation by distance. *Genetics*, 28, 114-138.

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