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The effect of isolation on Rock ptarmigan (*Lagopus muta*) population dynamics and genetics

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Introduction

Small, isolated or fragmented populations are exposed to a number of threats that can make them vulnerable to extinction including the loss of genetic variation, demographic and environmental stochasticity, and natural catastrophes (Shaffer 1981; Young and Clarke 2000; Beissinger and McCullough 2002). In addition, population persistence depends on the balance between emigration and immigration. The effects of these processes on population viability are well documented, both theoretically and empirically, although the relative role of each process is often debated (Lande 1993; Allendorf and Ryman 2002).

In alpine environments a number of species are limited only to the highest peaks, and individual populations are thus likely to be fragmented and/or isolated from each other. These effects are likely to increase in magnitude in years to come as global warming leads to advancing tree lines and a reduction of alpine habitat. Following these changes in habitat availability, a number of isolated populations will undoubtedly face the negative effects typical for small populations. For example, genetic drift (i.e. random loss of alleles) is expected to increase in small populations, resulting in the loss of evolutionary flexibility. As climate change proceeds, the ability to adapt to new environmental conditions will be of paramount importance and could determine whether populations disappear or species go extinct.

Moreover, severely isolated or fragmented populations might suffer from inbreeding or outbreeding depression. When populations become too small for individuals to successfully find a suitable mate (the Allee effect), individuals might breed with close relatives or with individuals of a closely related species. These maladaptive behaviours are likely to lead to offspring of low quality, with a reduction in population viability as the end result. Recent studies have also shown that many small, isolated or fragmented populations have a skewed operational sex ratio due to natal dispersal of only one sex, leading to a large proportion of unpaired individuals in the population (Dale 2001; Steifetten and Dale 2006). Consequently, the number of new recruits into the population will decrease, pulling the population further toward extinction.

Based on the problems that many small, isolated or fragmented populations face in an ever changing world the preservation of such populations poses a specific challenge to both conservationists and wildlife managers. However, one way to mitigate the negative effects of habitat fragmentation is to manage several small populations as one large "metapopulation", i.e. a network of fragmented populations interconnected by dispersal. This, on the other hand, requires that dispersal takes place. In the future, the ability to disperse will be extremely important for maintaining gene flow among populations (to increase genetic variation and to minimize inbreeding depression), and for recolonizing temporarily extinct populations. Unfortunately for most species that now have a fragmented distribution, little is known as to how, or even if individuals disperse, and if dispersal itself is enough to rescue those species from going extinct. Thus, knowledge of dispersal and its associated behaviours is crucial for understanding why some species are presently declining and how species will react to future environmental change. Last, but not least, knowledge of dispersal behaviour is important for the implementation of conservation measures.

The rock ptarmigan (*Lagopus muta*) occurs worldwide throughout the arctic and in many more southerly alpine regions as well. In Norway it occurs in most alpine regions, at or above tree line, throughout the year (Pedersen 1991). Though most populations appear to be non-migratory, rock ptarmigan are good fliers. Both insular populations, and populations on isolated mountain peaks situated tens of kilometers apart, are common throughout Norway. The amount of dispersal between these small, peripheral populations and more central populations has not been investigated in Norway or the rest of Fennoscandia. Though complete isolation seems unlikely, many peripheral populations may exist as sub-units in a functioning metapopulation, with reoccurring periods of extirpation followed by repopulation from neighbouring populations (Hedrick 1996). Alternatively, dispersal between sub-units may be so frequent that extirpation rarely, if ever, occurs. Rock ptarmigan in the Pyrenees appear to be genetically impoverished compared with those in the Alps and Norway, and display a greater divergence (Caizergues *et al.* 2003).

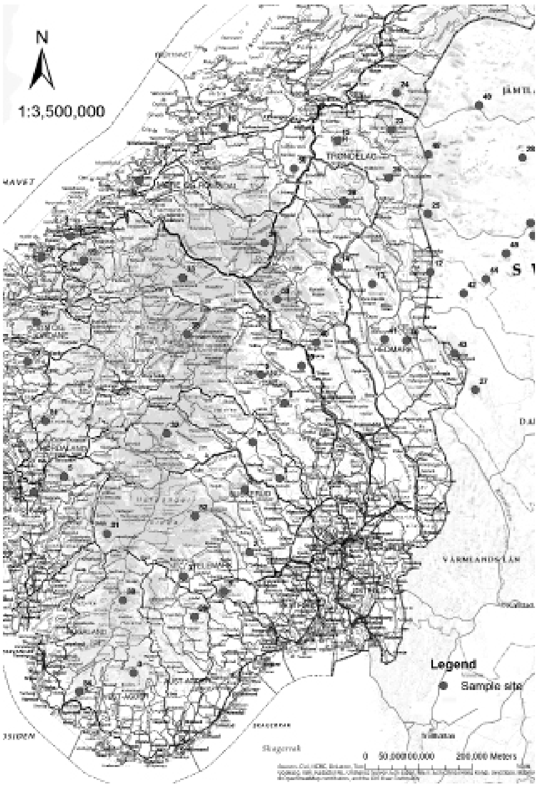

Fig. 1. Study area.

In the Alps, despite a weak genetic differentiation between localities up to 200 km apart, a significant isolation-by-distance effect was detected.

In Norway, human activity in alpine regions is increasing. Presently, rock ptarmigan can be legally hunted from the 10th of September through February in southern Norway. This combination of increased habitat loss, increased access and disturbance, coupled with unlimited hunting pressure, may be submitting isolated populations of rock ptarmigan to increased probability of extirpation. The successful management of these populations would benefit considerably from baseline information on their genetic composition and demographics (including dispersal behaviour).

The study

The main focus of the project will be centred on the population genetics and population dynamics of rock ptarmigan on isolated peaks in southern Norway (Fig. 1).

Population genetics: main goals

The genetic structure of different populations of rock ptarmigan in Norway will be analysed using microsatellites. The aim of the study will be to test how habitat size and degree of isolation affects genetic variability among populations, and hence their potential to adapt to new environmental conditions in the future. Following the "The Island Biogeography model", the null hypothesis will be that small and severely isolated populations will have low genetic variation, while large and less isolated populations will have higher genetic variation. Populations of intermediate size and with an intermediate degree of isolation are predicted to have a genetic variability that lies in between these two extremes. The results from this study will be compared with data on dispersal in the rock ptarmigan. Field work: Collection of primarily faecal pellets and moulted feathers on mountain tops throughout southern Norway as a source of DNA.

The degree and speed of genetic drift will be analysed using the same method as above. The aim of the study will be to see whether genetic variation changes over time as a function of habitat size and degree of isolation. Small and severely isolated populations are predicted to have the largest loss of alleles compared to large and less isolated populations. Field work: As above.

Population dynamics: main goals

The dispersal behaviour of rock ptarmigan populations will be studied using GPS telemetry. The aim of the study will be to examine if and how rock ptarmigan disperse in relation to several biotic (ptarmigan density and sex, food availability, small rodent density, hunting pressure, and other human disturbance) and abiotic (snow conditions, time of year) variables. Field work: Capture and fitting of GPS transmitters will be performed primarily during spring.

The operational sex ratio of individual populations of the rock ptarmigan will be studied through field observations and the collection of genetic material. The aim of the study will be to see if there is a lack of females (due to female natal dispersal) in isolated populations, and how this could affect population viability (e.g. the recruitment of new individuals into the population). Field work: Field observations of territorial males during the breeding season and the collection of faecal pellets for sex determination.

Effect of climate change on rock ptarmigan habitat: main goal

We predict that global warming will lead to a gradual advance of the tree line, thereby reducing the total area of rock ptarmigan habitat. This decrease in habitat area should, in turn, lead to reduced size of individual populations and increased distance between them (increased isolation). Present models of climate change that predict the effect of warming on tree line dynamics will be employed to predict future changes in the area and dispersion of rock ptarmigan habitat. Analytical methods: Geographical information system (GIS) will be employed to quantify the predicted rock ptarmigan habitat changes.

Acknowledgements

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