

Grouse – Habitat Relationships: Monitoring, Scale, and Management

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Cover: A childhood memory of capercaillie in Nautedalen, Lauvdal
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Abstract

Fennoscandian grouse populations are facing habitat degradation and are in decline, though not to the same degree as in western and central Europe. To be able to identify factors causing population decline and initiate proper management actions, a well functioning monitoring program and management are essential. In this thesis I have used datasets on capercaillie, black grouse and willow ptarmigan. The datasets were sampled through large scale monitoring programs by volunteers. The volunteers were mainly hunters that already had field-experience and knowledge of grouse, and could do the work at low cost and with few logistical problems. I found that using a GPS to measure perpendicular distances less than 50m from line transects reduced the reliability of the density estimates. Adding covariates such as habitat (open or closed), and flushed by dog or handler, improved the models of density estimates. In non-systematic sampling designs where hunters were free to go wherever they wanted during sampling, I found little bias in the habitat selection of hunters compared to that of capercaillie and black grouse, probably caused by the diversity in habitat use among the hunters. This indicates that such sampling of data can also provide unbiased indices of population density, given a sufficiently high number of hunters is used for monitoring. Based on the adult density and chick production from the density estimates, I found a positive relationship between the heterogeneity of the landscape and both adult density and chick production of capercaillie and black grouse. Forest of moderate to high productivity had a positive effect on adult density of both species while contrary to expectation the proportion of old forest seemed to have a negative effect on chick production of both species. I did not detect any clear relationship between willow ptarmigan and habitat at either the individual or the landscape scale. However, at the population scale habitat relationships were detected. Together, these results suggest that methods for monitoring grouse species are quite reliable, but could be improved by rather simple additions. Moreover, habitat composition seems to generate differences in demographic rates and population densities among populations, but these are not detectable at the individual or landscape scale. This suggests that management of grouse species should be done at a scale that captures the heterogeneity in the landscape, most likely over larger areas.

Keywords: habitat, *Lagopus lagopus*, *Tetrao urogallus*, *Lyrurus tetrix*, spatial scale, monitoring, management

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Dedication

To Roar, Sylva and Eivind

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List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I Lande, U.S., Hörnell-Willebrand, M., Willebrand, T., Solvang, H. and Pedersen, H.C. Using line transects and distance sampling to monitor Willow ptarmigan (*Lagopus lagopus*) (manuscript).
- II Lande, U.S., Herfindal, I., Finne, M.F. and Kastedalen, L. 2010. Use of hunters in wildlife surveys: do hunter and forest grouse habitat selection coincide? *European Journal of Wildlife Research* 56:107-115.
- III Lande, U.S., Herfindal, I., Willebrand, T., Moa, P. and Storaas, T. Adult density and chick production of capercaillie and black grouse in relation to landscape characteristics (manuscript).
- IV Lande, U.S., Willebrand, T. and Hörnell-Willebrand, M. Understanding the spatial distribution of willow ptarmigan – does habitat matter or not? (manuscript).

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1 Introduction

Within Fennoscandia, grouse (Tetraonidae) are found mainly in the boreal forest and alpine to sub alpine regions. They are directly exposed to human activity in terms of hunting, forestry, recreational development and agriculture. Capercaillie (*Tetrao urogallus*) and black grouse (*Lyrurus tetrix*) have declined over the last 20 – 30 years in central Europe, United Kingdom and parts of Fennoscandia (Storch 2007, Kurki et al. 2000). Bag statistics of willow ptarmigan (*Lagopus lagopus*) show a similar decline in Norway (Statistics Norway 2010). These declines are of great national concern in the individual countries which are required under international conventions (e.g. the Bern Convention) to carry out sustainable use and management of natural resources, such as wild flora and fauna and their habitats. All grouse species are subject to recreational hunting in Fennoscandia and management aims to ensure sustainable use. Land owners are interested in managing their grouse populations to increase the land use revenue (e.g. hunting licences with cabin rentals).

Wildlife habitat management has traditionally been focused on basic indices of cover, food and water. But wildlife – habitat relationships are far more complex, and research has greatly advanced the techniques for modelling the habitat of wildlife populations during the last 20 – 30 years (Morrison et al. 2006). I therefore consider the monitoring and management of grouse and their habitats as an important issue in this thesis. What is typical of grouse habitats and are we able to identify it?

1.1 The concept of habitat and niche

We are living in a constantly changing environment. Due to major human impact we are experiencing climate change which also leads to changes in ecosystems, landscapes and habitats (Parmesan and Yohe 2003, Rosenzweig et al. 2008). In this setting it can be argued that we are morally responsible to make sure that all use of wildlife and its habitats is sustainable. Already in 1859 Charles Darwin defined a habitat as the locality in which a plant or animal naturally lives. Today the most accepted and used definition of the term was provided by Hall et al. (1997); a habitat is defined as “the resources and conditions present in an area that produce occupancy – including survival and reproduction – by a given organism. This is wherever an organism is provided with resources that allow it to survive”. It is the sum of the specific resources an organism demands. Any place that holds the resources for the survival and reproduction of an organism is a habitat (Hall et al. 1997). Block and Brennan (1993) are more general and define habitat as a subset of physical environmental factors that a species requires for its survival and reproduction. In his book “Wildlife – Habitat Relationships” Morrison (2006) takes on a more scholarly definition which includes food, cover, water, temperature, precipitation, presence or absence of predators and competitors as important for the occupancy of an area, survival and reproduction of a species or a population. In other words habitat is organism-specific and not simply a vegetation type. Habitat use is defined as the use of biotic and abiotic components by an organism in a habitat (Hall et al. 1997). Block and Brennan (1993) define habitat use only slightly differently; the way an individual or a species uses habitats to meet its life history needs.

Developing rigid habitat models would provide us with tools to more effectively manage wildlife and wildlife habitats. Morrison et al. (2006) describe five main objectives for habitat modeling; 1) to formalize our current understanding about a species or an ecological system, 2) to understand which environmental factors affect distribution and abundance of a species, 3) to predict future distribution and abundance of a species (creating scenarios), 4) to identify weaknesses in and improve our understanding, and 5) to generate management or research hypotheses about the species or system of interest as a validation test of the modeling results. In this thesis I have focused mainly on objectives 2 and 4. In an attempt to identify specific factors affecting grouse distribution and abundance, I have searched for habitat relationships. It has also been important to evaluate the

monitoring data and the methodology to help us find weaknesses and strengths that will improve grouse management.

The niche concept has been described as the “profession” or “occupation” of an organism in an ecosystem (Odum 1959). Others consider a niche to consist of several axes (Hutchinson 1957) corresponding to different resources important to the animal, and then a combination of the “utilization distributions” of these resources is a niche (Levins 1968, Schoener 1974). Since there are elements in common when identifying the niche and the habitat of (e.g.) a species, the traditional wildlife – habitat relationships stays as the main concept in this thesis.

The development of habitat models seems to be heading into two directions, narrow species requirements or more broad landscape qualities. Single species models were early and often used to estimate food availability of different herbivore species. Since the beginning of habitat modelling around the 1980s a large variety of habitat models on more or less local (small) spatial scales have been developed. These are recognized by the question of optimal habitat and herbivores (Ball and Dahlgren 2002, Johnson and Gillingham 2005). Another set is more focused on the whole landscape and its structures. These models contain more broad scale habitat factors and resources. The selected species involved are examples (possibly keystone species) used to illustrate a landscape or region (Mouton et al. 2007).

Habitat models can be developed for all species if data on their existence and habitat requirements is available. Species differ in how narrow their habitat requirements are, and both generalists and specialists can be described with similar habitat models. A generalist is a species with a broad diet, while a specialist is one which prefers either one type or just a few types of foods (Begon 1996). Grouse are mainly habitat generalists. Popular species to model are focal species, e.g. “umbrella”, “flagship” and “keystone” species. The giant panda is a typical flagship species, its small population size is of great conservation concern (Qi et al. 2009). An umbrella species is a species for which the habitat covers the habitat for a great number of other species, in other words modeling habitat for conservation may benefit other species (e.g. grizzly bear; Servheen 1983, capercaillie; Storch 2000, Suter et al. 2002, Pakkala et al. 2003, Miettinen 2009). Keystone species or indicator species are species with resource needs that indicates a certain type of ecosystem (like the beaver and prairie dogs). Modeling all of these is of great

value to manage both single species and multiple species in a landscape or ecosystem.

1.2 Scale

Scale is an essential part of understanding wildlife – habitat relationships. Population processes occur at different scales for different species. To be able to analyse this properly our measurements of scale have to coincide with that of the organism(s) or species in focus (Wiens 1989). With spatial scale we often understand the location at which an analysis is taking place (Figure 1). It is important in relation to the habitat variables in the analysis to recognize if it is at a local/individual scale, regional/population scale or at landscape (large scale)/ecosystem scale. In the early 1970s Owen (1972) and Wiens (1973) recognized the concept of selection and selection at different spatial scales.

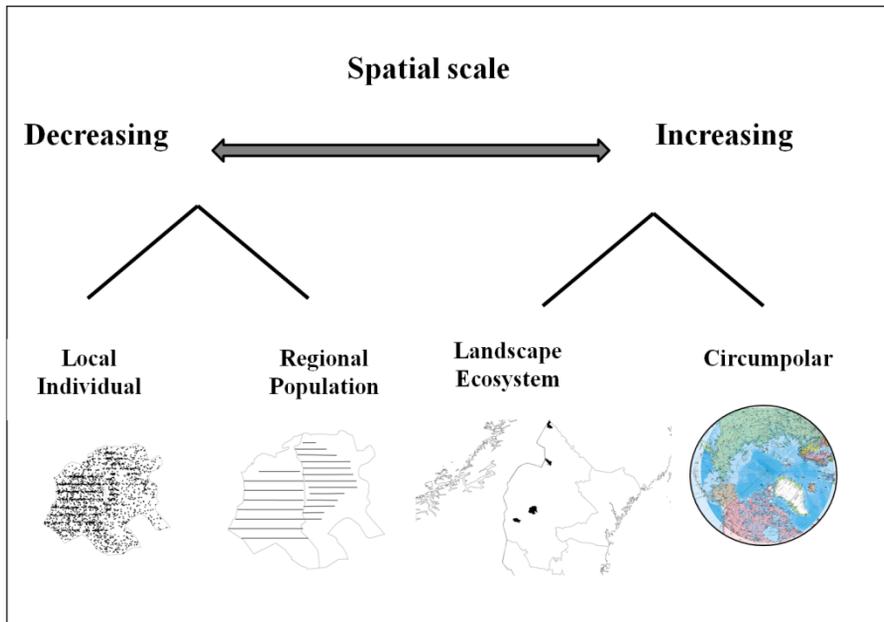


Figure1. Illustrating spatial scale of willow ptarmigan. GPS locations along line transects reflect the individual scale. Density estimates from a management area provide a population level. Several management areas within e.g. a county may serve as a landscape/ecosystem scale. The largest spatial scale of willow ptarmigan is its northern circumpolar distribution.

Selection of a habitat with certain resources, in this context, will be the process of one individual actually selecting one or more resources within

this habitat (Johnson 1980). One way of viewing selection is to divide it into several orders. A first order selection is the selection of the range of a species. A second order selection is the selection of a home range within the total range of the species. A third order selection is the selection of resources within a home range. At last, the fourth order selection considers the selection of types of foods among those that are available to the species (Johnson 1980). In a more general definition we can say that habitat selection is a hierarchical process of behavioral responses that may result in the disproportionate use of habitats to influence survival and fitness of individuals (Harvey and Weatherhead 2006). Habitat selection occurs at the individual level, and the distribution of a species or population is the sum of the selection of individuals.

Metapopulation theory has been applied to capercaillie and black grouse populations in central Europe and introduces an important spatial scale issue (Storch and Segelbacher 2000, Sachot 2002, Segelbacher et al. 2003). A metapopulation is defined as the population of populations when the range of a species is fragmented, and where subpopulations in more or less isolated patches are only connected through gene flow, extinction and recolonization (Hanski and Gilpin 1996). If the metapopulation is arranged as one or more patches being large enough to sustain permanent subpopulations while other subpopulations within small and unproductive patches face extinction it is called a source-sink system (Pulliam 1988). Willebrand and Hörnell (2001) developed a spatial model where they assume that harvesting grouse created a source-sink system where dispersal connected management areas with different harvesting strategies.

The temporal scale is simply what time period a model will be valid for. It is based on the time of the data put into the model, one time period or several (time-series). In the case of herbivore - habitat models a mix of temporal scales might be difficult to avoid due to seasonal or cyclic migrations, seasonal habitat use, cyclic habitat use, animal GPS locations, spring counts, hunter observations among others. Being aware of the different scales and describing them carefully during pre-modelling can greatly reduce the risk of misunderstandings or difficulties when interpreting modelling results. Some species defend their home range and show territorial behaviour. The resources defended can either be food, nest or denning sites, mates etc. In populations where contest competition is common, e.g. large carnivores, not all individuals can be expected to select the best habitats. In less territorial populations, e.g. grouse in Fennoscandia,

we would expect individuals to distribute more freely (ideal free distribution) and be found at the highest densities in the best habitats (Fretwell and Lucas 1969).

1.3 Monitoring

Population fluctuations of capercaillie and black grouse have attracted researchers and managers for a long time (Hagen 1952, Sivonen 1957). In Finland, transect counts (Finnish wildlife-triangles) and bag statistics have provided time series since 1964 (Lindén 1988). In Sweden, transect counts since 1960 exists (Hörnell-Willebrand 2005). In Norway, bag statistics from each county have been collected since 1972 (Statistics Norway 2010). Monitoring data have also been derived from research projects and large landowners (e.g. Statskog SF) in restricted study areas using telemetry data, lek censuses and hunting bags (Rolstad and Wegge 1987, Pedersen et al. 1999, Brainerd et al. 2005). Today there is an increase in the number of areas that participate in counting grouse using line transects and distance sampling (Solvang et al. 2009). In Norway today, these data cover 1400 km of line transects in the forested areas of mid, central and south Norway, but time series are seldom longer than ten years (Solvang et al. 2009). The quality of wildlife monitoring data is often measured by the length of time series, how well defined the survey designs are and the applicability of the data for management purposes (Gibbs et al. 1999).

There is a long tradition in both Norway and Sweden of managers and researchers working in close cooperation to develop sustainable ptarmigan management systems (Hörnell-Willebrand 2005, Tallmon et al. 2004, Brainerd et al. 2005, Solvang et al. 2009). The annual line transect counts of ptarmigan in Sweden and Norway are carried out by several hundred participants. This kind of voluntary activity is rare in Europe but quite common on game species in Fennoscandia (Lindén et al 1996, Elgmork 1997, Ericsson and Wallin 1999, Solberg and Sæther 1999, Hörnell-Willebrand 2005, Pellikka 2005, Mysterud et al 2007, Pedersen and Karlsen 2007). Motives for volunteers to participate in the counts include getting information about grouse densities and training their dogs during a time when it is not permitted elsewhere.

Distance sampling is an established method to produce density estimates of biological populations (Buckland et al. 2001). Data is collected either from line transects or point counts. The concept is based on data retrieval

on objects of interest at certain distances y_i from randomly placed lines or points. A detection function is then fitted to the observed distances, and this fitted function is used to estimate all the objects that the observer has failed to detect. The result is then an estimate of the density of all objects in the survey area. The amount of uncertainty in the density estimates lies in the assumptions of the detection function ($g(y) = \text{prob}\{\text{detection} \mid \text{distance } y\}$). A specific computer program (DISTANCE) has been developed for this task and is widely used (Buckland et al. 2001, Thomas et al. 2006). Distance sampling is an extended version of quadrat based sampling. In quadrat based sampling all objects are assumed counted within a circle of a point or an area of a strip (line). Using Distance sampling this assumption is relaxed and therefore more applicable to real life where we know it is almost impossible to detect all objects (Thomas et al. 2002).

There are some critical assumptions using distance sampling (Buckland et al. 2008). All individuals on the transect line are assumed to be detected with absolute certainty when distance sampling is applied to line transect counts. Being a “snapshot” method, Distance sampling also assumes the individual is detected at its initial location. Further; the perpendicular distances are measured exactly, if individuals occur in clusters the cluster size is counted exactly and the set of lines sampled are representative of the entire region surveyed (Buckland et al. 2008).

1.4 Hunting and Management

In Sweden and Norway, hunting is regarded as an integrated and important part of wildlife conservation (Bergström et al. 1992, Brainerd and Kaltenborn 2010). All game is essentially protected, and hunting can only take place to the extent and in the ways permitted by law. Hunting takes place to a greater or lesser extent on most land where it is legally permitted and Sweden has approximately 260 000 (Dept. of Agriculture, Sweden 2010) active hunters and Norway 143 000 (Statistics Norway 2010) active hunters. Grouse hunting in Fennoscandia is considered an important resource and is the most popular recreational hunt (Brainerd and Kaltenborn 2010). Every year 80 - 90 000 hunters in Norway and 10-20 000 in Sweden hunt for black grouse, capercaillie, hazel grouse (*Bonasa bonasia*) or willow ptarmigan (Statistics Norway 2007, Willebrand 1996), where black grouse and capercaillie are the most popular species in forested areas below the alpine vegetation zones. The hunt for willow ptarmigan dominates sub-

alpine and alpine areas, covering approximately 50 000 km² in Sweden (Statistics Sweden 2010) and 140 000 km² in Norway (Statistics Norway 2010). Capercaillie, black grouse and willow ptarmigan are all managed as game species in Fennoscandia.

Harvesting grouse has long traditions throughout Norway and Sweden, but willow ptarmigan were not readily accessible to hunters in Sweden before 1993 when the legislation changed for state owned land in the mountain range. In Norway, there is a more pronounced mix of landownership made up of state land and several smaller privately owned areas. Management of grouse in both Sweden and Norway is to a large degree concerned with monitoring, where results can be used to locally reduce the open season or impose a daily bag limit (Hjeljord 2008). The Scandinavian model for wildlife management and conservation has been proposed by eight guiding principles (for details see Brainerd and Kaltenborn 2010). These principles show that hunting and harvesting wildlife is applicable for the aim of wildlife conservation and management.

1.5 Studied species

All grouse species show large annual fluctuations and population dynamics, with variation in mortality of chicks and adult as the proximate cause which are influenced by multiple factors. One proposed explanation is the alternative prey hypothesis where generalist predators switch between grouse and voles depending on their relative abundance. Population fluctuations of grouse coincided with the cyclic fluctuations of voles (Hagen 1952, Linden 1988). Cyclic fluctuations have been observed to a much lesser degree during the last 20 years (Hörnfeldt 2004). This may be a result of climate warming leading to crashes in vole cycles and with an increase in generalist predators (Hörnfeldt 2004).

1.5.1 Capercaillie and black grouse

Even though the distribution of black grouse and capercaillie overlap to a large extent on a coarse scale, they are expected to be distributed differently within the forest system due to different preferences for forest successional stage (Seiskari 1962, Swenson and Angelstam 1993). Although habitat preferences in both species may show some seasonal variation (Swenson and Angelstam 1993), the main pattern is a preference for younger forest or even open moorland by black grouse whereas capercaillie are associated with

older pine/conifer forest. Spring and summer habitats are important for nesting success and chick production (Storaas and Wegge 1987, Rolstad et al. 1988, Willebrand 1988, Wegge et al. 2005). Both female capercaillie and female black grouse nest in a wide range of habitats, from clear cuts and bogs to old forest (Storaas and Wegge 1987). Hens with a brood use moist areas, like bogs and swamp forests, where the density of larvae and insects is high (Rodem et al. 1984). During late summer and early autumn when most monitoring occurs, grouse tend to change habitat from highly productive, moist and insect rich areas to older forests with well developed shrub and blueberry (*Vaccinium myrtillus*) layers (Storch 1993, Selås 2001). During autumn, the chicks fledge, but remain largely in their natal areas as clutches (Rolstad and Wegge 1989). These areas are preferred by both species until the snow comes. The winter habitat and lekking area for male capercaillie consists of more open forest with both Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) (Sachot et al. 2003), while female capercaillie prefer areas with younger and denser forests of Scots pine (Gjerde and Wegge 1989). Black grouse in general choose younger forest than capercaillie, and both birch (*Betula* spp) and bogs seem to be important factors for their habitat choice (Rolstad and Wegge 1989).

1.5.2 Willow ptarmigan

Willow ptarmigan is the only circumpolar species of the grouse studied in this thesis (Hannon et al. 1998). They are usually monogamous and remain in pairs from the breeding season until the chicks are independent. Willow ptarmigan are well adapted to their common environment in the alpine and sub-alpine region. Typical willow ptarmigan habitat consists of willow (*Salix* spp) and mountain birch (Hannon et al. 1998). During spring and until October/November the willow ptarmigan cocks defend a territory of 3 – 10 ha (Pedersen 1984). Nesting areas are usually placed within the territories of the cocks in the sub-alpine birch forest. When the broods hatch, the chicks depend on the insect and nutrition rich part of bogs and shrub layers at the edge of the birch forest tree line. As juveniles they switch to more vegetative nutrition in drier shrub and heath land, and as it becomes autumn berries make up a large part of the diet (West and Meng 1966). The winter diet is mainly willow buds and twigs (Hakkarianen et al. 2007).

1.6 Objectives

The main objective of this thesis is to evaluate the validity of the data collected for management purposes. This is important for management, but also to know the limitations when using such data in research (modelling habitat relationships), from which results can improve knowledge of willow ptarmigan, capercaillie and black grouse and benefit future management.

The main objective is addressed in four different papers where the aim of each was:

Paper I – To summarize the experiences of a large-scale monitoring program designed to monitor willow ptarmigan, a hunted species of conservation concern, and to investigate parts of the performance of Distance sampling methodology.

Paper II – To examine hunters' movements while searching for forest grouse, as well as locations for grouse observations, and to analyze the selection for habitat by hunters, as well as how this corresponds to the habitat preferences of black grouse and capercaillie.

Paper III – To investigate how landscape characteristics influenced two demographic rates (chick production per adult hen and adult density) in capercaillie and black grouse.

Paper IV – To investigate whether willow ptarmigan are clustered in the same locations from year to year and if available vegetation maps can be used to evaluate how suitable an area is for willow ptarmigan.

2 Material and Methods

2.1 Study Areas

Data were collected from study areas in both Norway and Sweden (Figure 2). In paper I we used data from 15 areas in Norway and 17 areas in Sweden. The Norwegian areas were distributed within Hedmark and Sør-Trøndelag counties, a mid and eastern mountainous region close to the Swedish border. The Swedish study areas consisted of eight areas in Norbotten, two areas in Västerbotten and seven areas in Jämtland counties. The areas are all located in the sub- and low alpine zones with low shrub vegetation, mainly dwarf birch (*Betula nana*) and willow, heaths, nutrient poor bogs and mountain birch forest (*B. pubescens.*) ranging from 500 – 1050 m.a.s.l. The Norwegian areas were situated closer to human settlements and roads than the Swedish areas due to a high degree of development in the sub- and low alpine zone in Norway.

The study of hunters, forest grouse and habitat selection (Paper II) was conducted in Østfold County. Østfold County, situated in the south eastern part of Norway, is 4 100 km² in total with a relatively flat topography ranging from sea level to 336m.a.s.l. Western parts are characterized by farmland and urban areas whereas the eastern and northern parts are dominated by forests of Norway spruce at lower elevation and Scots pine on ridges and bogs. The forest is subject to intensive commercial logging resulting in a heterogeneous landscape of clear-cuts and forest stands of different age classes. Urban and agricultural areas as well as open water were excluded from the analyses.

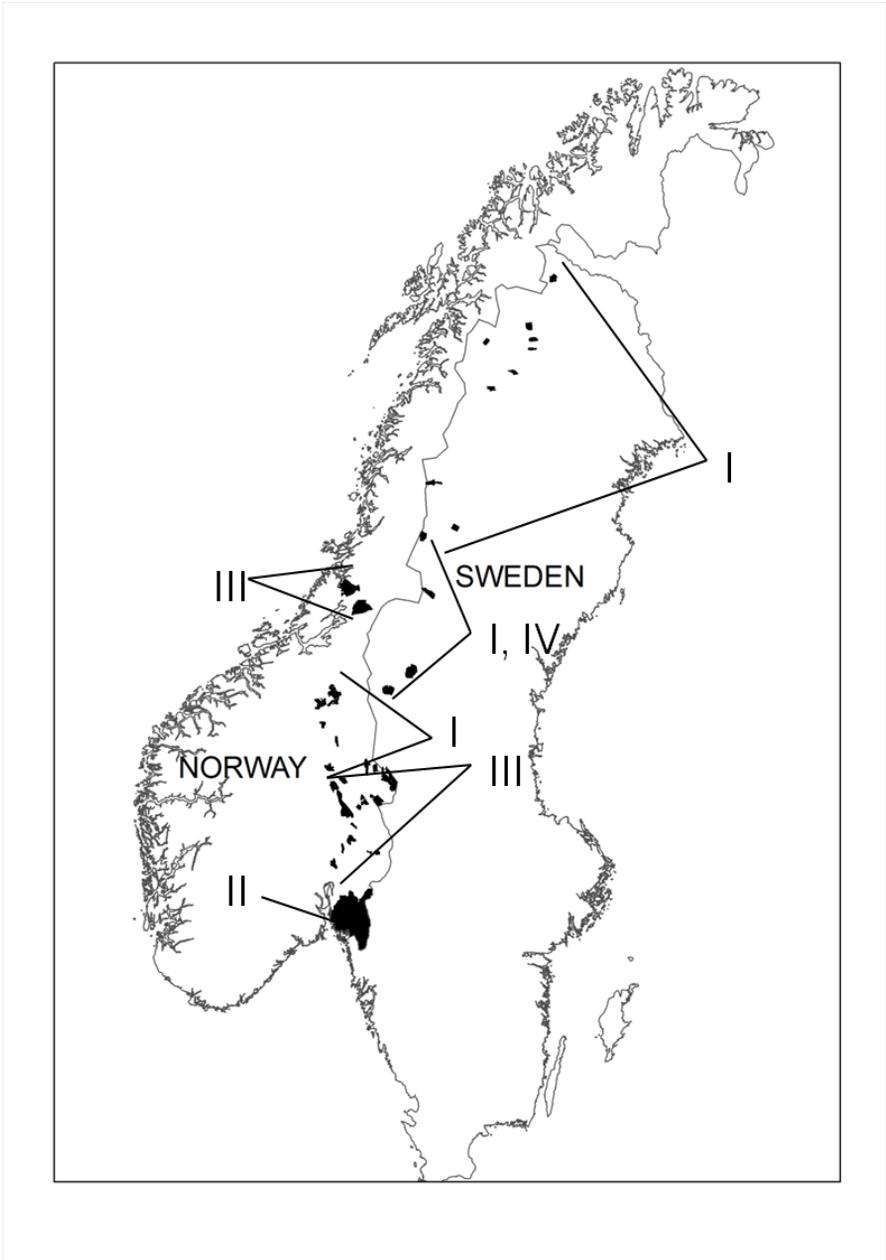


Figure 2. The geographic locations of all areas linked to each paper (I-IV) in this thesis.

Adult density and chick production of capercaillie and black grouse (paper III) were studied in 13 areas located Akershus, Hedmark and Nord Trøndelag County, Norway. Their sizes range from 11 km² to 370 km². The areas were mainly recognized by large continuous forest areas where Norway spruce and Scots pine dominate. With a varying topography the landscape will be heterogeneous in terms of forest age, structure and productivity. Human activity was present in the form of forestry, hunting and recreational activities (e.g. hiking, berry picking). The landscape characteristics chosen to best describe all the study areas and fit the preference of capercaillie and black grouse are described in table 1.

Table 1. The landscape characteristics describing the study areas and used to evaluate adult density and chick production of capercaillie and black grouse.

	Landscape characteristics	Description	Data source
Biotic factors	Mean forest patch size	Mean size of forest patches (stands) within each study area	SatSkog (Gjertsen 2007)
	Mid to high productivity forest	Proportion of forest cover producing more than 3m ³ ha ⁻¹ year ⁻¹	SatSkog
	Old forest	Proportion of forest with tree age > 80 years	SatSkog
	Simpsons index of habitat diversity (SiD) (Simpson 1949)	Proportions of spruce younger than 80 years and older than 80 years, the proportions of pine younger than 80 years and older than 80 years, the proportions of conifer mixed forest, deciduous forest and bog	SatSkog/AR 50 (Aune-Lundberg & Strand 2010)
Abiotic factors	Mean estate size	Mean size of estates within each study area	Digital estate map

When analysing willow ptarmigan habitat use (Paper IV), I used seven study areas derived from a previous study (Paper I), all located in Jämtland County, Sweden. Hotagen (area id 14, not hunted and 15, hunted) (63°59'N, 14°15'E), Flatruet (20, not hunted and 21, hunted) (62°02'N, 14°21'E), and Tassasen (18, not hunted and 19, hunted) (62°41'N, 13°17'E) are all located in the southern part of Jämtland and the central Swedish mountain range. Stekenjokk (26) (65°00'N, 14°30'E) is located in the

northern parts Jämtland. These areas are recognized by four main categories of mountain vegetation: heath, where dry heath is dominated by low shrubs as *Vaccinum myrtillus* and *Betula nana*; fresh and wet heath are dominated by larger shrubs such as *Salix* and juniper; meadow, tall and low herb meadows where grass and herbs dominate; a mix of bog and birch forest with lichens. On average the southernmost study area lies 872m.a.s.l., ranging from 631 to 1047m. Stekenjokk lies at average 664m.a.s.l., ranging from 525 to 927m. The climate for all areas featured warm summers and cold winters, with snow covering the grounds from November to April. Hotagen, Flatruet and Tassasen have been censused since 1996 and Stekenjokk since 1999.

2.2 GPS data

Twenty volunteer hunters with pointing dogs recorded grouse observations within Østfold County during August 2003 and 2004, prior to the start of the ordinary grouse hunt. The volunteer hunters were experienced grouse hunters recruited from a regional bird dog association. A hand-held GPS recorded the entire track of their hunting trips, and the locations of all flushings of black grouse and capercaillie were recorded manually with the GPS by the hunters. Subsequently one observation was taken every 30 m along each track. This ensured that the sampling regime was consistent between hunters and not dependent on minor differences on the GPS-units. The expected GPS error was between 5 and 15 m. The hunters were given no instructions about where to walk, and it is assumed that their spatial behaviour reflects their impression of what habitat characteristics provided the highest likelihood of encountering black grouse or capercaillie in order to train their dogs prior to the hunt. In total the volunteers walked 113 track days, 52 in 2003 and 61 in 2004. The hunters walked different tracks; the only overlap between tracks appeared when one track crossed another track. The median track length was 4140 m (min 1250 m, max 11600 m). In total 529 km of tracks were walked with an estimated search width of 20 m (Brittas and Karlbom 1990), covering approximately 21 km² ($\approx 0.8\%$ of the forested area in Østfold).

2.3 Density estimates

The line transect counts for all three grouse species were conducted during the first two weeks of August by volunteer hunters with pointing dogs

(Hörnell-Willebrand 2005; Solvang et al. 2009). Both countries use permanent lines, visiting the same set of transects each year. The volunteers are carefully recruited; they are trained and evaluated every year in Sweden, whereas in Norway, after being given a basic course, they are trained more sporadically (Solvang pers. com.). In both countries one person keeps track of the transect line and one person with one dog searches for birds (Pedersen et al. 1999, Hörnell-Willebrand 2005). However, in Norway it is quite common with two or more persons and two to four dogs per transect, but rarely with more than two dogs searching simultaneously.

The dataset of density estimates and chick production (young per adult) of capercaillie and black grouse were based on line transect sampling during 2002 – 2009. Not all areas participated from the start in 2002 and counts with data from at least three years were used in the analysis. On average 241 transect lines were censused (range 155 to 302) per year. One transect line was on average 3.4km with a range from 2 to 5.6km. Each transect line in all areas was censused with a minimum of two volunteers and a pointing dog in late July or early August each year. Volunteers were recruited and trained to census a set of a priori chosen lines within each area (see Solvang et al. 2009 for more details). More details on line transect sampling and obtaining distances to observations is explored in detail by Buckland et al. (2001). All estimates were calculated by the software program Distance (Buckland et al. 2001).

2.4 Statistical methods

Mixed effects models (Bates 2010) were used to analyse possible effects on willow ptarmigan encounter rate (Paper I), to evaluate the effect of the habitat factors on adult density and chick production of capercaillie and black grouse (Paper III) and to analyse whether encounters of willow ptarmigan are more clustered than expected from chance (Paper IV). Mixed effects models include the typical response variable in relation to one or more covariates measured in respect to the response. Important for these types of models is that at least one covariate has to be a random effect of categorical type. This categorical covariate represents observational or experimental units in a dataset e.g. study area. Random and fixed effects, parameters associated with levels of a covariate, are recognized in mixed effects models (Bates 2010).

Estimates of adult density were log plus one transformed due to left skewed data and zeros (Paper III). The estimates of chick production remained untransformed. Observations will show interdependence within year and study area, and we accounted for this by adding year and study area as random factors in all models. We ran multi-species models for adult density and chick production since both species are quite synchronous and are censused at the same time and place. The global model for both adult density and chick production consisted of mean forest patch size, the area of the study area, the proportion of old forest, the proportion of mid to high productivity forest, Simpsons index of habitat diversity (SiD), the interaction mean forest patch size and Simpsons index of habitat diversity all in interaction with species as a factor (capercaillie = 0 and black grouse = 1). Study area and year were treated as random factors (Table 1) in all models. Mean estate size was removed from the global models as it correlated (Pearson's $r = 0.84$) with mid to high productive forest.

We used AIC, corrected for small sample size (AICc, Burnham and Anderson 2002), to rank alternative candidate models (Paper I and III) with the lowest AICc corresponding to the best model. A difference in AICc (ΔAICc) of less than two between alternative models suggests that these should be considered as equally good (Burnham and Anderson 2002). We used AICc-weights (the probability that a model is the best, given the set of candidate models) and evidence ratios (i.e. the favour of model A being better than a candidate model B; $\text{AICc-w(A)} / \text{AICc-w(B)}$) to evaluate and rank candidate models (Burnham and Anderson 2002). The AICc was calculated from models fitted using maximum likelihood (ML), whereas parameter estimates are based on models fitted with restricted maximum likelihood (REML) (Zuur et al. 2010). A type of principal components analysis (see below) was used for analysing hunters, grouse and habitat selection (Paper II).

ENFA (Ecological Niche Factor Analysis) is closely related to principal component analysis and calculates an ordination of data in a multivariate space with environmental variables (Paper III). The technique is used to find the main factors explaining the distribution of a species in an environment. These main factors are summarized from the environmental variables and have a biological significance. The factors can be divided into two groups; 1) a marginal factor, the marginality, and 2) tolerance or specialisation. Based on the multi-dimensional space of habitat characteristics, the marginality will indicate a measure of the distance from the hunter-selected habitat to the

average environmental profile of the study area. Thus, the marginality identifies preferences of used versus available habitat (Basille et al. 2008). The tolerance or specialisation factors are based on the variance in the distribution of the available habitat characteristics compared to the variance in habitat that is used. A high specialisation indicates that the individual or population is utilising a narrower range of habitat values than what is available. This is related to the placement and width of the realised niche space compared to the biotope space, as defined by Hutchinson (1957). A method relative to the ENFA and also based on the ecological niche is the K-select method, designed for habitat selection analyses (Calenge et al. 2005). K-select performs a non-centred principal component analysis of the table containing the coordinates of the marginality of each animal (row) on the habitat variables (column), and returns a linear combination of habitat variables for which the average marginality is greatest (Calenge et al. 2005). K-select results in a combination of variables which contribute the most to the habitat selection. Accordingly, K-select results do not consider specialisation, but visualise the habitat selection at different spatial scales, where the axes correspond to the first and second axis of marginality.

Potential clustering of willow ptarmigan on transect lines among years was analysed by taking the average harmonic mean of distances for each point to all other points of encounter along a line (Paper IV). For each line, this value was compared to the average harmonic mean for the same number of random distances as ptarmigan encounters. Differences close to 0 suggest no clustering, and values larger than 0 indicate a tendency for ptarmigan to occur clustered between years. Preference and avoidance of habitat classes by individual willow ptarmigan were analysed in a contingency table (Zar 1998). Habitat relationships at the population and ecosystem scale were graphically explored rather than statistically analysed due to small sample size. All statistical analysis were made using R (R Development Core Team 2010).

3 Results and Discussion

3.1 Monitoring Grouse (I, II)

Distance sampling of willow ptarmigan in Norway and Sweden are conducted in slightly different ways, which makes the inference of the results from wildlife monitoring more challenging. This was partly founded in the goals of willow ptarmigan management in each country. In Norway the density estimates are used at a local management level as well as at the county level to estimate hunting quotas or bag limits. In Sweden the results are used to monitor population development, and evaluate if the management model used is supported by the data. Both the size of the monitoring areas (Sweden mean 76.38 km (SD = 19.45) vs. 41.7 (SD = 30.48) km in Norway), and the line transect lengths 5.85 km (SD = 2.52) vs. 3.12 km (SD = 0.64) were larger in Sweden than in Norway. On the other hand number of encounters per kilometre transect were higher in Norway compared to Sweden, on average 0.97 (SD = 0.34) and 0.62 (SD = 0. per kilometre. Densities of willow ptarmigan were on average more than twice as high in Norway compared to average densities in Sweden, 30.1 (SD = 16.94) vs. 14.68 (SD = 9.95) per km². The Swedish data contained a larger proportion of the perpendicular distances close to the line compared to the Norwegian data, mean 59.26 m (SD = 59.66) and mean 75.13 m (SD = 66.91) respectively. There was a significant positive relationship between density and total transect length in the Swedish material ($F = 5.61$, $df = 186$, $P = 0.019$) that was not present in the Norwegian data ($F = 2.89$, $df = 80$, $P = 0.093$).

Factors that may affect these estimates are the use of GPS, temperature during the sampling period and covariates for the flushings (e.g. habitat and flushed by dog or handler). We found that the average difference between

paced out distances and GPS-measured distances to the same encounter was 6.7m (SD 6.1, max 31m), in favour of the paced out distances. At short distances the relative difference between the GPS and the paced out distances was most pronounced. High temperatures had no significant effect on the encounter rate (CPH, likelihood ratio test= 0.77, df=1, P=0.38). In terms of trying to improve the detection function and thereby the density estimates, we introduced covariates; open or closed habitat, flushed by the dog or the dog handler. The best model fit included both habitat and how birds were flushed.

After evaluating the line transect sampling and distance sampling methodologies for large scale monitoring of willow ptarmigan in Norway and Sweden, we would recommend pacing out the perpendicular distances and careful use of a GPS. If choosing to use a GPS one has to be aware of the possible bias introduced by GPS location error for shorter distances (< 50m). An option is to adopt the Finnish method where the distances are paced out and then controlled afterwards using the track log of a GPS (Hörnell-Willebrand pers. com.). Contrary to previous belief, high air temperature did not lower the dogs' ability to locate willow ptarmigan. Including covariates such as habitat type may improve density estimates. Recording open or closed habitat is now routinely done in the monitoring of willow ptarmigan in Norway and Sweden. The personnel sampling the majority of these data are volunteer hunters which results in work done at low cost and with minimal logistic problems. It provides local involvement and a better understanding of important management tasks required by the hunting regulations; it increases the communication and reduces the gap between researchers and stakeholders (e.g. hunters and landowners).

In paper II we examined the use of having hunters conducting wildlife surveys on capercaillie and black grouse. Based on hunter knowledge and experience we expected hunters to be selective in their use of forest stands, particularly with respect to tree species, tree age and density/visibility closely related to the traditional grouse habitat defined by Seiskari (1962). In addition we expected the frequency of encounters with grouse to depend on the habitat type, and to be different for black grouse and capercaillie. The analysis involved determining how the habitat characteristics of the locations where grouse were observed differed from the hunters' habitat selection, as a measure of habitat selection of grouse conditional on the hunters' habitat selection. A large variability in habitat utilisation between the hunters was revealed. Medium tree volume and low productive conifer

forest were the only two habitat variables selected for by several of the hunters. The majority of the hunters selected against non-forest areas, Norway spruce, deciduous forest and high productive conifer forest. Black grouse was positively related to pine forest, high conifer productivity, and high tree volume. Capercaillie was positively related to high tree volume and normalized difference vegetation index (NDVI). For both species pooled high conifer productivity, non-forest, high tree volume and pine forest were positively related variables. The analysis showed that the habitat selectivity among individual forest grouse hunters differed substantially (Table 2).

Table 2. The selection frequency (number of hunters that did not select, selected for or selected against the different habitat characteristics) of the habitat variables included in the ENFAs run on individual hunters. (M is the vector of marginality along the variable axis representing difference in used habitat compared to the available).

Habitat type nr.	Variables		Not selected ($ M < 0,20$)	Selected for ($M > 0,20$)	Selected against ($M < -0,20$)
1	Tree volume	Low (Vol 1)	20	0	0
2		Medium (Vol 2)	11	7	2
3		High (Vol 3)	6	5	9
4	Tree type	Non forest (Vol NF)	2	0	18
5		Norway spruce	6	5	9
6		Scots pine	15	5	0
7	Productivity	Deciduous	1	4	15
8		Mixed forest	11	4	5
9		Non forest (Tree NF)	12	0	8
10	Bog	Bog	8	6	6
11		Non bog	20	0	0
12	Impediment	Non forest (Prod NF)	9	0	11
13		Impediment (Imped)	15	2	3
14		Low (Prod 1)	12	7	1
15		Medium (Prod 2)	12	5	3
16		High (Prod 3)	5	6	9
17	NDVI		20	0	0

This suggests that hunters' behaviour with respect to optimizing habitat use for grouse encounters could not be considered as a general behaviour, but rather depends on the individual hunter. Assuming that these hunters are representative, between them they will cover most of the habitat types in relation to the composition of the landscape due to the hunters' individual habitat utilization. Our study indicates that observational data by hunters, in a sufficient number, can be used as one additional index in the attempt to monitor forest grouse population dynamics. Their habitat use is representative of the total area and therefore quite useful for monitoring capercaillie and black grouse in late summer/early fall since these species use a wide range of the available habitat without showing a strong habitat selection.

3.2 Habitat and scale (III, IV)

In paper III adult density and chick production were modelled in response to the proportion of forest older than 80 years, proportion of mid to high productivity forest, mean forest patch size, mean estate size, study area size and an index describing the diversity of the landscape (Simpson's index of diversity, SiD) (Table 1). Both species were included in the models for a comparative study due to the species being sympatric and showing a high degree of spatial and temporal synchrony. The highest ranked model explaining variation in adult density of capercaillie and black grouse among the study area included Simpson's index of diversity and the proportion of mid to high productivity forest. Both Simpson's index and mid to high productivity forest had a positive effect on adult density of both species (Figure 3). In addition we controlled for the random effects, year and study area. These two factors explained 4.8% and 7.2% respectively of the total model variation.

The highest ranked model explaining chick production of capercaillie and black grouse included SiD, proportion of old forest, species, and the interaction Simpsons index of diversity and species. SiD had a positive effect on chick production, and due to the interaction it was slightly more positive for black grouse than for capercaillie. The proportion of old forest had a negative effect on chick production of both species (Figure 4). The random effects, year and study area, explained 34.7% and 14.6% respectively of the total model variation.

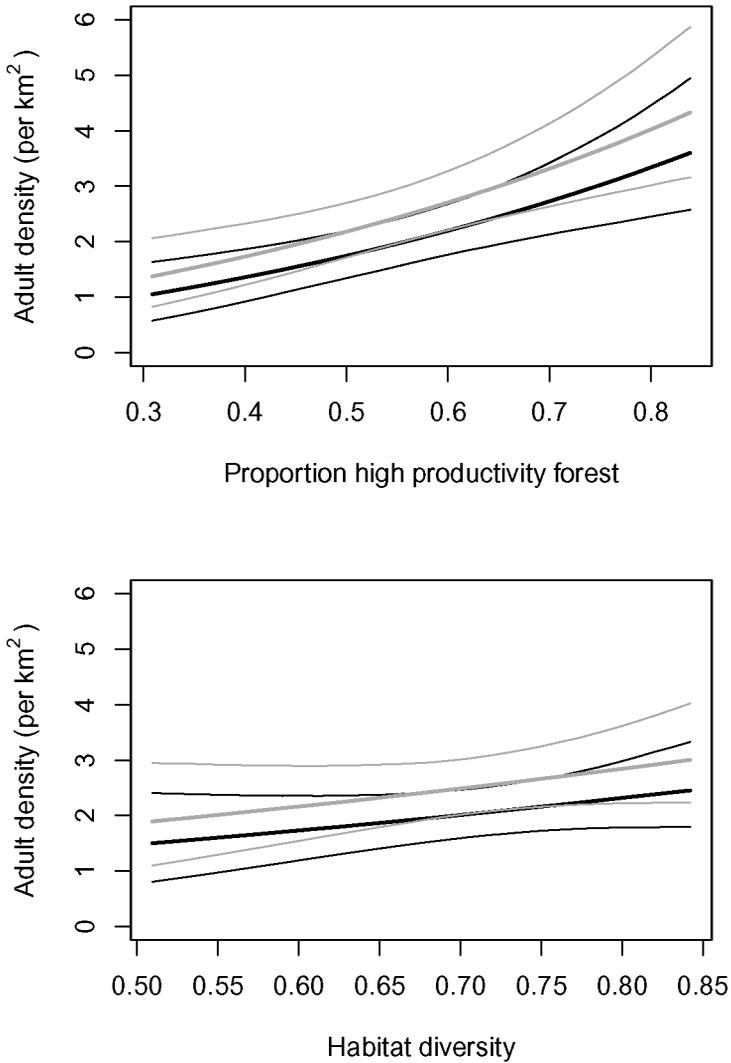


Figure 3. The relationship between adult density of capercaillie (black lines) and black grouse (gray lines), and the proportion of mid to high productive forest and habitat diversity (SiD) based on the highest ranked model according to AICc (Table 2). The thin lines represent 95% confidence intervals based on the 2.5% and 97.5% quantiles from 10 000 MCMC resamplings from the posterior distribution of the parameter estimates.

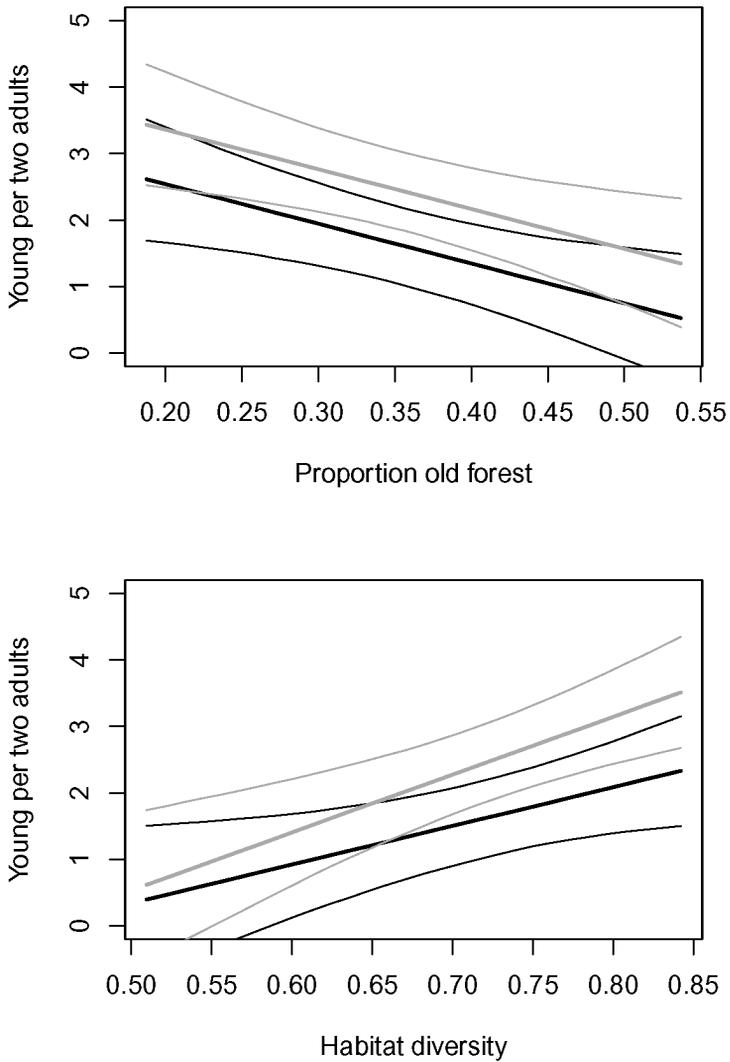


Figure 4. The relationship between chick production of capercaillie (black lines) and black grouse (gray lines), and the proportion old forest and habitat diversity (SiD) based on the highest ranked model according to AICc (Table 2). The thin lines represent 95% confidence intervals based on the 2.5% and 97.5% quantiles from 10 000 MCMC resamplings from the posterior distribution of the parameter estimates.

These results indicate that capercaillie and black grouse seem to be quite similar in how habitat at the landscape scale influences demographic rates. A positive effect of the Simpson's index indicates that a heterogeneous landscape, consisting of a variety of both young and old spruce and pine forest, mixed forests, deciduous forest and bog, is beneficial for both adults and chick production. In other words, in a heterogeneous landscape, there is enough old forest presumably preferred by capercaillie and enough open areas (bogs and younger forest) favoured by black grouse. Mid to high productivity conifer forests are characterized by rich moist soil cover at these latitudes, and can easily meet the demands for both capercaillie and black grouse throughout most of the year. To secure adult survival and recruitment of capercaillie and black grouse, an area has to possess the habitat demands serving both of these vital rates. Adult survival of both capercaillie and black grouse are related to human disturbance in terms of surviving the hunt and the winter season with its limited nutrition, weather conditions and predators (Kurki et al. 2000, Wegge et al. 1987).

We considered willow ptarmigan habitat at the individual, population and landscape (multiple populations) scales (paper IV). Hunters report that willow ptarmigan tend to be located in clusters especially during the hunting season (autumn). As predicted, we found that ptarmigan encounters were significantly more clustered than random locations, with the exception of two out of seven areas. Habitat selection at the individual scale was analyzed in a contingency table, where an avoidance for birch and a preference for bog was found ($\chi^2=55.95$, $df=3$, $P<0.001$). Ptarmigan were found in equal proportion to random locations within alpine heath and alpine meadow.

At a population level, we found that adult densities in neighbouring areas showed consistent differences. Adult density was always higher in the hunted part of 14&15 ($t=4.8$, $df=12$, $P<0.001$), while the opposite was true for area 18&19 ($t=6.3$, $df=13$, $P<0.001$) and 20&21 ($t=1.5$, $df=13$, $P=0.15$). When introducing the four habitat classes from the individual scale we found an apparent pair-wise difference in habitat classes in relation to the difference in adult density. An increasing proportion of alpine heath was positively related with higher willow ptarmigan adult density, while an increase in both the proportion of bog and birch were negatively associated with adult density (Figure 5, first row). At the landscape scale, the relationship between the relative difference in adult density and the relative difference in habitat classes disappeared (Figure 5, second row).

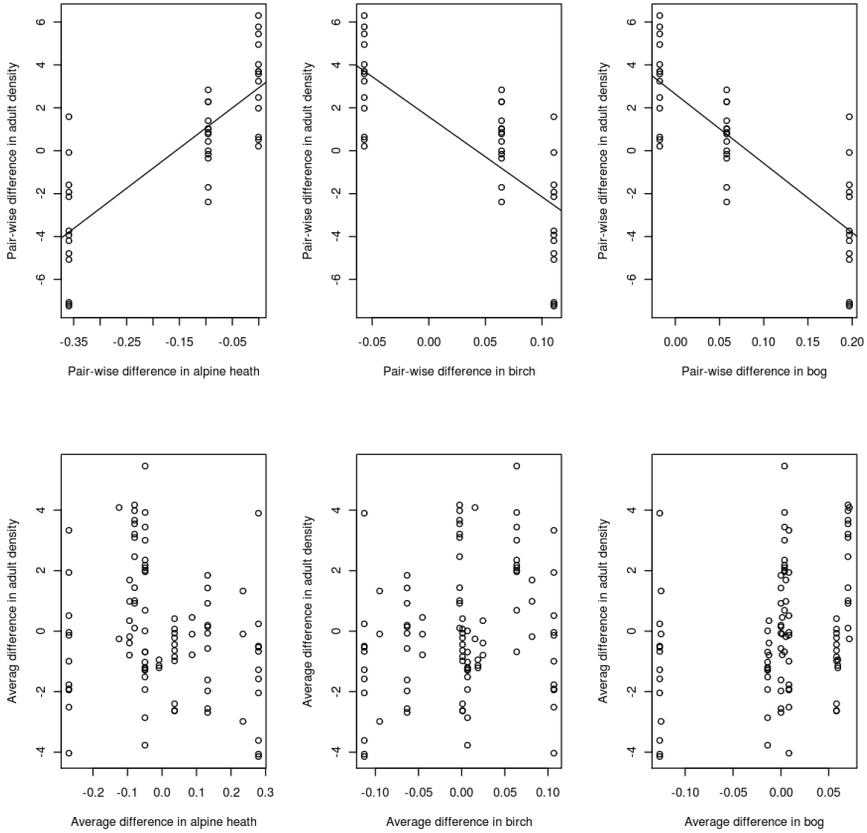


Figure 5. The relationship between major habitat classes and adult density. The first row shows the annual differences in adult densities between pair-wise areas, and pair-wise difference in proportion of habitats. The second row shows the annual differences in adult densities in relation to the overall average for all seven areas, and the difference in proportion of habitat classes compared to the average habitat composition for all seven areas. All lines represent the slope from a linear regression.

Both the results of forest grouse (capercaillie and black grouse) and willow ptarmigan point towards demographic rates as important measurements to understand habitat relationships. Therefore, the next step is to recognize the appropriate spatial scale at which the data should be analyzed for future management. Since several mechanisms interact and affect demographic rates (e.g. mortality, reproduction, immigration and emigration), and these may operate at different scales, we need to manage grouse at a scale that ensures the inclusion of these mechanisms. For willow ptarmigan, our findings indicate that a spatial scale large enough to contain the dispersal ability of females (6 – 10km) (Hörnell-Willebrand and Smith unpubl. data) may be optimal. A relationship between habitat classes at the population scale and adult density was apparent, but this was not the case when considering a larger, multi-population scale.

4 General conclusions

Knowing habitat use is important for precise wildlife management at appropriate scales, and that management should be knowledge-based. We therefore need both reliable data as well as knowledge about species. In this thesis I have evaluated data that serve as a basis for management of grouse in Fennoscandia. I used this data to obtain a better understanding of how grouse are related to habitat at different spatial scales. This is important because habitat alteration is one of the main threats to species diversity and maintenance (Kålås et al. 2010).

Modelling wildlife habitat relationships is a complex issue (Åberg et al. 2000). Not only does the study species move, but habitats are dynamic and constantly being disturbed by natural and anthropogenic forces at different scales (George and Zack 2001 and references therein). The grouse habitat relationships analysed in this thesis does not support any findings at a species-specific individual scale. The methods as well as the approach could be wrong, or the scale may not be viewed with the right eyes. What are we missing? On the other hand, the willow ptarmigan habitat association could be assessed at the population scale. At this scale, the data on both willow ptarmigan and forest-dwelling grouse showed a close relationship between estimates of demographic rates and the habitat composition of an area. Consequently, it is possible to detect landscape characteristics that influence and generate differences in density among areas. This can also be used to predict impact of habitat degradation on the grouse populations, because it is possible to relate a specific habitat component to demographic rates. Since habitat diversity was important it appears grouse are able to cope with degradation in their landscapes, as long as diversity is maintained at the appropriate scale.

I evaluated the quality of data used for grouse management. The methods which are currently used to estimate grouse density or get indices of variation in density are quite reliable. However, they can easily be improved by simple additions. Consequently, the data from these methods should serve as reliable sources of information which is valuable both for management and research. However, anyone who uses the data should be aware of possible limitations. The system of grouse monitoring in Fennoscandia could be successfully applied in other areas, particularly areas with a decline in or unknown status of grouse populations. It would also probably give reliable estimates for other species (Wegge and Storaas 2009). A possible limitation, however, is the access to volunteers with sufficient training that can perform the rather high workload at a low cost, and qualified persons that can analyze and evaluate the data gathered. Nonetheless, if these challenges are overcome, I suggest these methods can provide valuable tools for species monitoring of a variety of species and areas.

To sum up, I would propose that grouse management should aim for management areas that are not too small (for willow ptarmigan at least 50km^2) or too large (not more than 500km^2 for willow ptarmigan). By taking into account that the demographic rates (e.g. dispersal) determine the scale, we may get both monitoring data that are easy to apply and wildlife habitat relationships that are possible to detect. The results show unambiguously that management could be improved; similarly, management at small scales is not recommended!

5 Management Implications

Precise management of a population should be knowledge-based and occur at an appropriate scale. The issue of scale in grouse management has, to a certain degree, been set by the sizes of the areas covered with line transects for monitoring. As we have seen in this study, the size varies quite substantially and the amount of results related to habitat and population densities also vary. What could then be drawn from this? Managers as well as researchers have to be aware of scale being locally dependent. A management area holding a viable grouse population in the southern part of a county may not be large enough for a viable population in the north of the same county. As my results suggest, habitat-grouse relationships was detected at the population scale while I was unable to detect relationships at individual and landscape scale. This could e.g. be due to climate, predator distribution, degree of habitat fragmentation, impact of human interference, soil and bedrock conditions. Accordingly, the appropriate scale for management should include areas that capture all these processes. The size of this may be landscape specific, for example due to the topography or heterogeneity of the landscape. However, management should at least be done at a population scale.

Hunters are interested and volunteer to provide important data outside the hunting season. With education, training and feedback, they can perform large scale and long-term monitoring not possible otherwise. However, if conservation of a species or sustainable harvest are the management goals, such designs of monitoring programs are dependent on a clear stated aim, proposed and lead by local management to generate local interest and engagement. Problems may arise with small areas, short line transects and few line transects which may result in e.g. overestimating

densities. As for line transect sampling with distance sampling methodology, the evaluations so far have created a set of guidelines possible to follow providing e.g. density estimates reflecting the real populations with a high level of accuracy (Buckland et al 2008, paper I). Similar systems now in Norway, Sweden and Finland make it possible to detect international trends in grouse fluctuations and meta-analysis of how ecosystem factors like predators and climate change affect grouse at a large spatial scale.

6 Future Perspectives

When analyzing monitoring data from line transect sampling, the data are at both individual and population scales. A consequence of this is that the aim of the research has to be focused on the two specific levels. In habitat modeling, the habitat variables or classes have to be sampled with a resolution that fits with the species-specific data. Individual habitat preference does not fit with a map of vegetation in 1x1km grid cells! There are varying amounts of available data on vegetation, bedrock, forest inventories, human infrastructure, grazing pressure and even landscape classes (e.g. Esseen and Löfgren 2004, Pushmann 2005). Problems often arise as data even within a country do not follow a unified classification system. This makes it difficult for wildlife biologists not familiar with all types of vegetation classes to know how these can be generalized. Another consideration is using data obtained from satellites (Suchant and Braunisch 2004, Breidenbach and Braunisch 2008) since these most often are seamless and not dependent on administrative borders, but may need ground truthing.

In Sweden, a system of National Inventory of Landscapes (NILS) was established in 2003 (Ståhl et al. 2010). The landscape monitoring program NILS provides suitable data for wildlife – habitat relationships in Sweden, an idea which could easily be interpreted in neighboring countries sharing the same wildlife species populations and facing the same management issues. A closer cooperation between institutes and expert groups may help facilitate this, and thereby contribute to taking habitat modeling to the next level, at least for grouse in Fennoscandia.

Climate change has not been an issue of this thesis, but it is highly relevant for wildlife habitat. Climate affects ecosystems both directly and

indirectly (Sjögersten and Wookey 2009). One factor which indeed will and has an impact on grouse population is the latitudinal and altitudinal shifts in vegetation types that can occur with increasing temperatures. For example an increase in tree line altitude of birch forest will affect willow ptarmigan while an increase in conifer tree line will affect capercaillie and black grouse. Climate change may also induce changes in predator - prey communities and parasite burdens.

Wildlife – habitat relationships have been and are proven difficult to identify and make statistical inference from. A major improvement would be to make predictions based on well formulated hypotheses taking spatiotemporal scale into account. The possibility of modeling a whole ecosystem is tempting, and to try to validate such a model. A grouse example; the relative density of grouse could be modeled as a function of habitat type, bedrock, soil, predators and climate. Altering some of these variables could give an indication of how the species would respond to changes in e.g. climate. However, since this may be very complex, reliable predictions rely on high-quality data, maybe even at the individual level.

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