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The Occurrence of Hazel Grouse in the Boreal Forest

Effects of habitat composition at several spatial scales

Johan Åberg

The occurrence of hazel grouse in the boreal forest: effects of habitat composition at several spatial scales

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Abstract

This thesis presents data on factors determining the occurrence and dynamics of hazel grouse populations at several spatial scales in five landscapes with different management regimes.

In a forested area with a low degree of habitat variation, the relationship between occurrence of hazel grouse and type of habitat was best explained at scales equal or larger than the home range, compared to smaller spatial scales. At this spatial scale the hazel grouse preferred spruce stands 20-69 years old and those older than 90 years, having 5-40% deciduous trees. More specifically the presence of hazel grouse in a habitat patch was positively influenced by a high amount of vertical ground cover, rich field layer vegetation and the presence of alder.

At the landscape scale the occurrence of hazel grouse in habitat patches in intensively managed landscapes was negatively affected by increasing distance between suitable habitats both in an agriculture-dominated landscape and in a forest-dominated landscape. The threshold distances for hazel grouse movements were about 200 m in the agricultural landscape and about 10 times longer in the forested landscape, suggesting a strong effect of different types of matrix. The dynamics of hazel grouse occurrence in habitat patches in the intensively managed forested landscape, were determined by distance to nearest suitable habitat patch, amount of cover in the habitat patch and habitat patch size. In a fine-grained less intensively managed landscape, using a 21-year long data set, habitat size and isolation were also found to strongly affect the presence of hazel grouse. Hazel grouse occupancy increased considerably in habitat patches larger than 10 ha. However, the effect of isolation occurred at a smaller spatial scale and was not induced by distance, instead it occurred as an avoidance of open land surrounding the habitat patch.

A high concordance, about 85%, between predicted and observed occurrence of hazel grouse was found when the models developed in the two differently managed forested areas were used on independent data from a third landscape.

The results presented in this thesis suggest that the hazel grouse is a poor disperser, avoids open areas, and has very specific habitat requirements, many of which conflict with production of coniferous pulp and timber. Theoretical aspects of landscape ecology and specific guidelines, including applicable measurements and evaluations of forest descriptions for maintaining the species in managed boreal landscapes, are discussed.

Key words: Conservation biology, forest management, habitat selection, hazel grouse, heterogeneity, landscape ecology, model testing and spatial scale.

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Contents

Appendix

Papers I-VI

The present thesis is based on the following papers, which will be referred to by their Roman numerals.

I.   Åberg J., Jansson G., Swenson J.E., Mikusinski G. 2000. Difficulties in detecting habitat selection by animals in generally suitable areas. Wildl. Biol. 6, 89-99.

II.   Åberg J., Swenson J.E., Angelstam, P. The habitat requirements of hazel grouse (*Bonasa bonasia*) in managed forest and applicability of forest stand descriptions as a tool to identify suitable patches. *Submitted manuscript.*

III.   Åberg J., Jansson G., Swenson J.E., Angelstam P. 1995. The effect of matrix on the occurrence of hazel grouse (*Bonasa bonasia*) in isolated habitat fragments. Oecologia 103, 265-269.

IV.   Åberg J., Swenson J.E., Andrén, H. 2000. The dynamics of hazel grouse (*Bonasa bonasia*) occurrence in habitat fragments. Can. J. Zool. 78, 352-358.

V.   Saari L., Åberg J., Swenson J.E. 1998. Factors influencing the dynamics of occurrence of the hazel grouse (*Bonasa bonasia*) in a fine-grained managed landscape. Cons. Biol. 12, 586-592.

VI.   Åberg, J. Predicting the occurrence of hazel grouse (*Bonasa bonasia*): a test of two models. *Manuscript.*

Introduction

Anthropogenic alteration, loss and reduced sizes of natural habitats, in combination with increasing distances between the remnants, are important causes of the decline in biological diversity in boreal forests (DeGraaf and Miller 1996). The rate and the scale over which the disturbances occur are often far greater than those normally produced by natural events (Wiens 1990) and the few remaining remnants of pristine forest are situated in a matrix of managed forest in different succesional stages (Wiens 1990, Hansson 1992). The consequences for the organisms inhabiting these landscapes often have been shown to be severe, because the composition and dynamics of the pristine forest differs essentially from the appearance and dynamics of the more or less managed forested landscape (Franklin and Forman 1987). And, as a consequence, many species have become extinct or are highly threatened (Gärdenfors 2000) in at least parts of their present distribution. Society has paid attention to the loss of species (SOU 1992). The objectives of the current Swedish forest policy declare that maintenance of biodiversity in forested areas is as important as the economic value of the forest and implies that all naturally occurring species should be found in viable populations. During the 1990's forestry and society have made efforts to achieve these goals on the scale of separate trees and forest stands (Anon. 1999), as well as on the level of landscape (Angelstam & Pettersson 1997). However, large gaps still remain in the knowledge of species' habitat requirements, species' responses to different forestry management practises at different scales, and what kind of forestry data is needed to conserve or restore biodiversity.

The forested landscape

The appearance and dynamics of the pristine boreal forest was clearly influenced by fire, a selective force (due to topography and geology) strongly influencing the development of the vegetation (Zackrisson 1976, Opdam 1990). This was a prerequisite for the long-term stability of vegetation successions over large areas, as well as on small areas (Esseen et al. 1992). Thus, the absence or low interval of fires on some sites and more common fires of different intensities on other sites caused a mosaic of differently affected forests (Zackrisson 1977). On a smaller scale, wind and snow also have an important influence on the pattern and dynamics of the pristine forest, especially on moist and wet sites (Skoglund and Verwijst 1989). The pristine boreal forest normally has a well developed vertical structure, both in number of trees and number of tree species (Majewski et al. 1995).

The intensity of forestry differs considerably among areas in Sweden due to ownership and economical interests, but some specific features can be

distinguished. The management of forests includes felling of mature forest and most often a replacement by plantations of a single conifer species, with a rotation time between 70-100 years. This results in forests with few old stands and a low amount of dead wood (Zackrisson and Östlund 1991, Esseen et al. 1992). Within the rotation time, several thinnings and removal of deciduous trees has contributed to a mosaic of more or less uniform, one-layered stands completely dominated by coniferous trees (Harris 1984, Hunter 1990). Thus, the management of forested areas has a strong impact on the appearance of forests both on the stand level and on the landscape level. The consequences vary by species and are generally poorly known.

Structural consequences of habitat fragmentation

Habitat fragmentation implies a subdivision of a certain habitat into several habitat fragments, a loss of habitat and microhabitats, a changed microclimate in the habitat fragments, and increased isolation (Wiens 1990, Saunders et al. 1991). This has lead to a reduction in the number of individuals of some species and in the total number of species (Dorp van and Opdam 1987, Verboom et al. 1991, Redpath 1995). Also, even seemingly uniform expanses of habitat, such as old forest, are really a mosaic of different habitats, at some level of discrimination. Therefore it is neccesary to identify the appropriate spatial and temporal scale (Wiens 1995) to detect a response to living organisms due to habitat fragmentation (Heads and Lawton 1983, Väisänen et al. 1986, Lord and Norton 1990).

As mentioned previously, another impact of habitat fragmentation is the loss of habitat continuity, i.e. insularization, but this phenomenon has to be distinguished from habitat loss *per se* (Rolstad 1991, Andrén 1994). The proportion of suitable habitat that is left has been proposed to greatly influence a species' response to habitat fragmentation (Andrén 1994). Forman and Godron (1986) stressed the importance of the matrix for the pattern and dynamics of populations in fragmented habitat. Matrix can be defined as the area element that exceeds the sum of the areas of all the other elements, connecting and surrounding the independent elements and may consist of anything but the habitat suitable for the species (Stamps et al. 1987). The quality of the matrix is likely to influence the distances an individual moves, and thereby the colonization rates of the habitat islands within the matrix (van Dorp and Opdam 1987), with edges of moderate contrast being more permeable (Wiens 1990).

Responses of animals to habitat fragmentation

Habitat fragmentation has negative effects on some species, but some are affected more than others (Wiens 1990, Bright 1993). Species that are most sensitive to changes in the structure of the habitat and landscape have been

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suggested to be those that occur at relatively low densities before habitat alteration and fragmentation occurs (Wilcox 1980), are sedentary, habitat specialists (Opdam 1990), occupy late successional forest habitats (Gotteli and Graves 1990), and have a low dispersal ability (Pimm et al. 1988, Kareiva 1990, Bolger et al. 1991, Wiens 1995). Vagile species are less affected by the habitat configuration, instead the total amount of habitat is more likely to be important to them (Pulliam and Danielson 1991).

A population decreases on a small as well as on a large scale (Villard and Taylor 1994). The proportion of suitable habitat in a landscape has been shown to be a critical factor influencing species occurrence in habitat fragments, at least when the proportion of suitable habitat left in the landscape exceeds 30% (Andrén 1994, 1996, Fahrig 1997). In addition, dispersal, proposed to be a key factor for the occurrence of species in spatially divided landscapes (Lidicker 1975, Greenwood 1980), may be hindered by the species' behavior, e.g. the degree to which they will traverse a hostile matrix surrounding a habitat remnant (Opdam et al. 1984, Dunning et al. 1992, Taylor et al. 1993, Gascon et al. 1999).

Tools for management of biodiversity

A prerequisite for promoting biodiversity in forests is knowledge of species' habitat selection at different spatial scales and at different densities, and habitat descriptions of good quality. In addition, reliable methods to follow changes in density and use of existing inventories of habitat are of great value. A common approach to create models for use in animal conservation and management has been to link known habitat use with maps of existing vegetation (Verner, Morrison & Ralph 1986). In general, the predictions of such models are often more successful if the species' habitat breadth is small (Edwards et al. 1996) and if the species is adapted to slow changes in habitat structure (Beshkarev et al. 1994). The accuracy of such a model should preferably have been evaluated using independent data (Rotenberry 1986). Moreover, before applying a successful model, the modeller should decide the objective of the modelling together with a stated acceptable error, how this error can be measured, and how the possible explanations for these errors should be ranked (Starfield 1997). Another approach in conservation biology has been the use of different indicator systems (Morrison et al. 1992), where the occurrence of a selected species is used to define habitats and/or rank their suitability for a certain species community. However, the system has its disadvantages (Jansson 1999) and may be risky if misused in conservation work (Caro and O'Doherty 1998).

Objectives of this thesis

The objectives of this thesis were to document habitat selection and effects of habitat alteration on hazel grouse (*Bonasa bonasia*) in different managed boreal landscapes at different levels of spatial scales, by:

1) Determining the relative importance of stochastic and deterministic factors for habitat selection at spatial scales also smaller than hazel grouse home ranges in a generally good environment, and how the spatial scale of measurement may influence the pattern of habitat selection using forest stand descriptions and additional vegetation descriptions (Paper I),

2) Evaluating methodological problems when measuring habitat selection in order to predict the occurrence of the species, and evaluating the applicability of forest stand descriptions and a censusing technique for managing of the species (Papers I and II),

3) Determining the habitat preference of hazel grouse at the size of a home range, in an intensively managed and forested area (Paper II)

4) Evaluating the importance of matrix for the occurrence of hazel grouse in habitat fragments in differently composed and managed landscapes (Papers III-VI),

5) Analysing the dynamics of occurrence of hazel grouse in habitat fragments in forest landscapes managed at different intensities in relation to the size and isolation of the habitat fragments (Papers IV and V),

6) Determining hazel grouse occurrence and dynamics in relation to amount of habitat left in the landscape (Papers IV-VI),

7) Testing the predictions from studies of the occurrence of hazel grouse in two differently managed landscapes, in a third landscape (Paper VI),

8) Presenting useful ecological data on hazel grouse for a long-term conservation of the species in managed landscapes (Papers I-VI).

Methods

Study areas

The studies were conducted in Sweden and Finland at different spatial scales in a gradient of landscapes managed at different intensities, composed of different amounts of more or less suitable habitat (Fig. 1). The study concerning the influence of stochastisity, habitat heterogeneity and spatial scale for determining hazel grouse habitat selection (Paper I) was performed in a recently inaugurated forest reserve in south central Sweden. The forested landscapes in south central Sweden, around Grimsö Wildlife Research Station, (Paper II, III and IV) are, and have been intensively managed for production of timber and

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pulp for several centuries, and only a very low proportion of suitable hazel grouse habitat is left in the landscape.
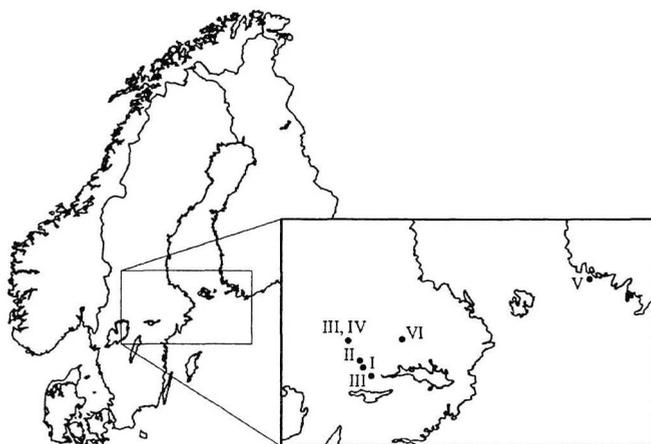

Fig. 1. The study areas used in Paper I-VI. Paper II, III and IV was conducted in intensively managed forested landscapes in south-central Sweden near Grimsö Wildlife Research Station. The studied area in Paper I was a forest reserve called Grönbo, in south-central Sweden. Paper V was conducted in a less intensively managed landscape at Aasla, an island in the south-western Finnish archipelago and, finally, the studied area in Paper VI was a privately owned forest dominated area in south-central Sweden near Sala.

The forested parts in the agriculture-dominated landscape in south central Sweden (Paper III) was low, and the intensity of forest practises in the areas is low. The type of matrix clearly differed between the above two mentioned landscapes. In the forest-dominated landscape matrix consisted of non-suitable forest and in the agricultural-dominated landscape matrix consisted of non-suitable open fields. In paper V a less intensively managed landscape was studied at Aasla, an island in the South-western Finnish archipelago. This landscape has the highest amount of suitable hazel grouse habitat of the studied landscapes in this thesis. The forestry practices are not, and have never been, very intensive on the island. The model predictions from papers III and V were tested in an area near Sala in south central Sweden (Paper VI). The forest in this landscape was owned by several private landowners and therefore the forest was managed at different levels of intensity. The proportion of suitable hazel grouse habitat in this landscape was intermediate in comparison to the landscapes studied in Papers III and V.

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The studied species

The hazel grouse is a small (375-400 g) forest-living grouse, distributed throughout the Palearctic boreal and montane forests from the western coast of Norway to northeastern Siberia and southwards into central France and North Korea (Bergmann et al. 1996, Swenson and Danielsen 1991). Occurring in relatively low densities, the very well-camouflaged, grey-brown spotted bird is hard to find, but the males territorial song may expose it.

The hazel grouse has the narrowest niche of the forest grouse living in the Palearctic boreal forest (Seiskari 1962, Swenson and Angelstam 1993), where it originally inhabited old-growth spruce forests with a multi-layered structure and a consistent supply of deciduous trees on fairly nutrient-rich soils (Eiberle and Koch 1975, Beshkarev et al. 1994). Suitable cover, mainly Norway spruce (*Picea abies*), with a high degree of canopy closure, and a thick understory of saplings for avoidance of predators, e.g. goshawk (*Accipiter gentilis*) and marten (*Martes martes*) is probably also important (Swenson 1991a, Swenson & Angelstam 1993). The preferred winter food in Fennocandia is catkins and buds of deciduous trees, preferably alder (*Alnus glutinosa* and *A. incana*) and birch (*Betula pubescens* and *B. pendula*) (Swenson 1993a). Female hazel grouse are also highly dependent on the availability of herbs (e.g. *Viola* spp., *Anemone nemorosa*, *Potentilla erecta*, *Oxalis acetosella*) and cottongrass (*Eriophorum vaginatum* and *E. angustifolium*), during the pre-laying period (Ahnlund and Helander 1975, Swenson 1991a).

The hazel grouse has been shown to be sedentary, very site-tenacious and having a very low dispersal ability (Swenson 1991a and b, Swenson and Danielsen 1995). The size of the hazel grouse territory, ranging from 20-40 ha per pair, depends on the quality of the habitat and is defended through most of the year, but the degree of defence varies and is most pronounced in autumn and spring (Pynnönen 1954, Swenson 1991a). The hazel grouse pair can be described as a co-operative alliance based on mutual benefits, such as increased survival due to vigilance from predators and increased chance of having a potential mate the following mating season (Swenson 1993b). However, hazel grouse males do not participate in the care of the relatively large brood (Swenson 1991a, Swenson and Boag 1995). Hazel grouse males, also juveniles, sing spontaneously and respond to the song of other males in spring and autumn (Swenson 1991a).

The hazel grouse has experienced a general decline in population size in Western and Northern Europe, with extinction in areas of Central Europe (Swenson and Danielsen 1991). A decline has also been documented in Japan (Fujimaki 2000). Changes in habitat structure, due to intensive forestry, are probably one of the main reasons for the decline of hazel grouse populations, but large-scale changes in habitat composition on a landscape level also are likely to have negatively influenced hazel grouse populations.

Vegetation data and censusing method

Traditional Swedish forest stand descriptions provided by the landowners in combination with other maps, for instance transformed infrared aerial photographs (Papers III and IV) and topographic maps, were used in all studies but the one at Aasla. There, a simplified vegetation map of suitable hazel grouse habitat, based on a topographical map and knowledge from the field, was constructed (Paper V). In addition to these maps, the field layer composition (Papers I and II), and the horizontal and vertical cover (Papers I, II, III, IV and VI), were measured in field.

The territorial vocalisation of hazel grouse males can be imitated with a hunter's whistle and, the occurrence of hazel grouse in an area can be determined, by walking along parallel transects 150 m apart, stopping at 150-m intervals and imitating the territorial song of hazel grouse males. This method, which was described and used in most of these thesis studies except Paper V discovers about 82% of all territorial males within 100 m during mid-April to mid-May and between mid-September to mid-October in central Sweden, as determined from radio-marked birds (Swenson 1991c). In Paper V hazel grouse were censused regularly during 21 years, by walking routes and transects, covering the total study area twice a month all year around. The observations, visual or aural, of individuals and broods were recorded on a topographical map (scale 1:20 000).

Results and discussion

Influence of habitat heterogeneity and stochasticity on habitat selection

No clear preferences for specific habitat types or structures were found range in a forest reserve with generally good hazel grouse habitat at the spatial scales (3.4-20 ha) smaller than hazel grouse home range (Paper I). This was, in spite of long-term data on a specialist species and detailed habitat descriptions (two 314m^2 plots per ha) covering a study area that was more than 25 times larger than an average home range of a hazel grouse (Paper I). The general lack of relationships was probably due to the following factors: 1) The habitat composition in general was probably suitable or acceptable (Haila et al. 1996) for the hazel grouse throughout the study area, in particular in the western part. That is, the qualitative differences between habitats were so small that territories could be established more or less anywhere. 2) The seemingly stochastic pattern of hazel grouse occurrences was most likely also related to the small scales analysed and the accuracy of the censusing method, which did not give the exact position of the censused hazel grouse male. 3) The amplitude of the density variation, or the difference between low and high years, was perhaps too small to

detect an effect in the richer and more suitable western area. Generally, within an area composed of overall suitable habitats for the focal species, and at scales analysed smaller than the species' home range, clear patterns of habitat preferences may perhaps not be expected.

Importance of spatial scale

The results of the habitat preferences at the smaller spatial scales (>20 ha) suggested that at least the scale of territory size (about 20-40 ha for hazel grouse) is a proper level to investigate possible patterns of density dependent habitat selection in a species. At smaller scales, the occurrence of individuals is more stochastic (Paper I). Some significant relationships between habitat variables and occurrence of hazel grouse were found when censusing habitat patches having a size similar to the size of a hazel grouse home range in an intensively managed forested landscape (Paper II, Table 1).

Table 1. Results of a one–way ANOVA, testing the three principal components, and the original habitat variables that were significantly different between source- and sink-, source- and non-habitat, and sink and non-habitat patches based on hazel grouse occurrence. Significant differences in mean values among the type of habitats are marked with asterices, where * = $p<0.05$, ** = $p<0.01$ and *** = $p<0.001$ (Paper II).

	Type of habitat		
	Source $n=18$	Sink $n=13$	Non-habitat $n=40$
PCA 1, plantations	0.21	-0.44	0.15
PCA 2, high pine component	-0.36	-0.03	0.12
PCA 3, dense low vertical cover	0.87***	0.13	-0.32***
Dead trees laying	2.83*	1.74	1.54*
Vertical cover, 4-10 m	2.58**	2.39	1.91**
Proportion cowberry	73.11*	87.62	91.40*
Proportion ground cover	1.80**	1.39	1.23**
Proportion pine	36.50**	51.62	65.70**
Proportion spruce	49.33*	40.92	27.85*
Prop. of deciduous trees	13.56***	7.46	1.78***
No. of spruce per ha	727.83*	439.46	394.85*

Note: Three patches were excluded when the effect of proportion of deciduous was analysed.

Differences in habitat suitability were distinguished by hazel grouse also at the larger scales i.e. at the scale of several home ranges, because the amount of

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cover of deciduous and coniferous trees in the habitat fragments (1-30 ha) (Papers II, III, IV and VI) and the amount and suitability of the surrounding habitat significantly influenced the dynamics of hazel grouse occurrence in the habitat fragments (Papers V and VI).

The suitability of matrix has been shown to influence hazel grouse occurrence strongly i.e. at the small scale of tree species composition in a pristine forest (Beshkarev et al. 1994) and in managed forests (Lindén and Wikman 1983). The suitability of matrix also influenced the occurrence of hazel grouse at the spatial scale of several home ranges in the small-scaled managed landscapes (Papers V and VI). There, hazel grouse occupied only habitat areas surrounded mostly by forested land. And, furthermore, an effect of matrix was found at the scale of groups of home ranges in the two intensively managed landscapes, one dominated by forested land and the other dominated by agricultural land (Paper III). Here, a ten-fold difference in possible colonisation rate for hazel grouse was found between the two landscapes.

Habitat preferences and habitat patch size

The proportion of pine significantly, and negatively influenced the occurrence of hazel grouse at the scales of home range and smaller (Papers I and II, Table 1). The proportion of deciduous trees was significantly higher in source habitats than in non-habitats, when patches having higher proportion than 50% deciduous trees were excluded (Paper II). The above two relationships indirectly suggest that an increasing proportion of spruce probably positively influences the occurrence of hazel grouse.

Shrubiness, a measurement of cover, was significantly and positively related to the occurrence of hazel grouse during autumn at the scale of a half home range in the western part of the reserve (Paper I). Moreover, amount of cover was also an important feature separating source habitats from non-habitats (Paper II), and the occurrence of hazel grouse during autumn was positively influenced by cover in the intensively managed forest area (Paper IV).

A positive influence of alder on the occurrence of hazel grouse was found in Paper II, where source habitat patches significantly more often contained alder than sink patches. And, no hazel grouse were found in habitat patches without alder in the small-scaled managed landscape in Sala (Paper VI).

No effect of patch size was found for the occurrence of hazel grouse in habitat patches larger than the home range size of hazel grouse (Paper II). However, when the censused habitat patches were smaller and more varied in size (1-30), the mean size of deciduous patches with hazel grouse in the intensively forested landscape was larger (9.2 ± 5.4 ha) than patches without hazel grouse (4.9 ±4.4 ha) (Paper III). Similar results, 11.2 ±7.4 ha for occupied patches, and 3.4 ±4.2 for unoccupied ones, were found in Paper VI. Not only the presence of hazel grouse males but also the probability to detect a hazel grouse

brood increased rapidly with increasing size and were significantly higher in habitat patches larger than 10 ha (Paper V). Thus, a threshold, where the occupancy rate increased rapidly, was apparent at about 10 ha in all the forested landscapes (Papers III-VI).

The importance of matrix

Simulation models have predicted that when the contrast between habitat and matrix is high, i.e. the edge permeability is low, species occurrence is mainly influenced by the distance to other habitat (Stamps et al. 1987). The comparison of hazel grouse occurrence within two intensively managed and fragmented landscapes, where both had a low proportion suitable hazel grouse habitat but where the type of matrix differed largely (Paper III, Fig. 2 and 3), gave support to this prediction.
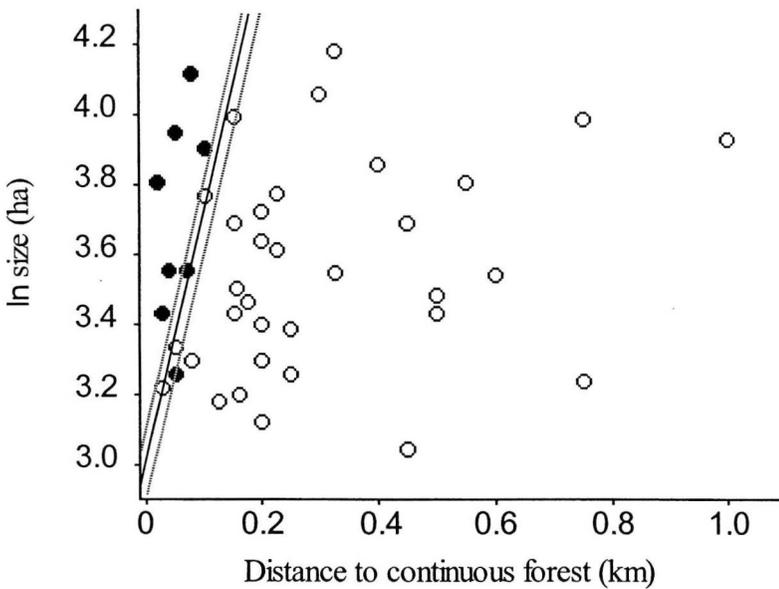
Fig. 2. Relationship between hazel grouse occupancy in habitat fragments surrounded by agricultural fields and distance to nearest continuous forest habitat and habitat fragment size, spring and fall 1990. Filled dots represent habitat fragments occupied by hazel grouse. Above the solid line the probability of hazel grouse occurrence is >50%, based on the logistic regression equation. The upper dotted line shows the 75% probability and the lower the 25% probability. (Paper III).

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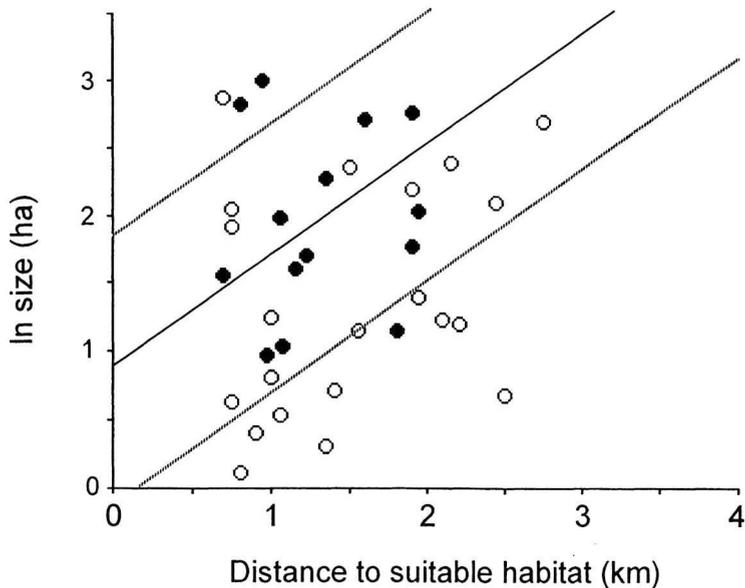
Fig. 3. Relationship between hazel grouse occupancy in habitat fragments surrounded by managed forest (non-habitat) and distance to nearest habitat fragment/continuous forest habitat and habitat fragment size, spring and fall 1992. Filled dots represent habitat fragments occupied by hazel grouse. Above the dolid line the probability of hazel grouse occurrence is >50%, based on the logistic regression equation. The upper dotted line shows the 75% probability and the lower the 25% probability. (Paper III).

The dispersal distance for hazel grouse differed 10-20-fold, with the most pronounced isolation effect in the landscape with hard edges i.e. an edge between forest and farmland. Thus, the study confirms the importance of matrix, stated by e.g Stamps et al. (1987) and Wiens (1995), and strongly suggests that the dispersal ability of hazel grouse were greatly influenced by the quality of the matrix.

Effects of isolation on hazel grouse occurrence in managed landscapes

The distribution of hazel grouse in the agricultural landscape showed distinct isolation effects (Fig. 3) (Paper III). An effect of isolation was also found for the occurrence of hazel grouse in the intensively forested landscape (Fig. 4) (Papers III and IV) and in the small-scaled managed landscapes (Papers V and VI). This is a surprising result, because modelling results of avian distribution in

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habitat mosaics predict species distribution only rarely to be influenced because of the species' vagility (Urban and Shugart 1986). Isolation effects have been found very rarely in empirical studies from forested landscapes (Andrén 1994, Villard et al. 1995, Reunanen et al. 2000). However, few of these studies were conducted in landscapes with a sufficiently low proportion of remaining suitable habitat, where effects might be found, and the scale of where effects can be expected were not always satisfactory (Andrén 1994, 1996). Also, the species-specific habitat requirements have great importance for the possibility to study this event (Kareiva 1990, Paper III).

The occurrence of hazel grouse in habitat fragments of different isolation and size, and during different seasons, was studied and analysed. Habitat fragment size was most important for the distribution and the total number of hazel grouse in a habitat fragment, irrespective of season, explaining about 20% of the variation in hazel grouse occurrence (Fig. 4). However, adding distance from the nearest suitable habitat fragment to the multiple stepwise regression model increased the explanatory power of the model by a significant 11% for autumn and the combined seasons, but not for spring. (Paper IV)
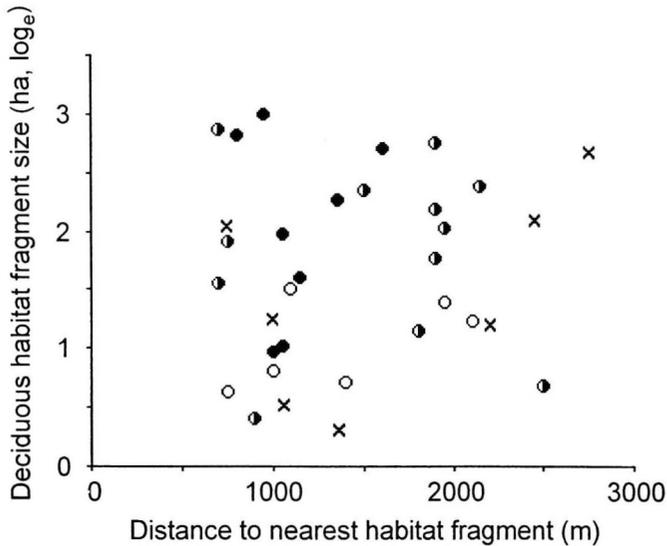

Fig. 4. Relationship among the number of seasons that hazel grouse occupied a habitat fragment from spring 1992 to spring 1995, habitat fragment size (log; ha), and distance to nearest habitat fragment. Solid circles represent habitat fragments occupied by hazel grouse during four or more seasons, half solid circles represent fragments occupied two or three seasons, open circles represent fragments only occupied once and crosses represents unoccupied fragments during seven seasons.(Paper IV)

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In the two less intensively managed landscapes, Aasla and Sala (Paper V and VI), habitat area was the most important factor influencing hazel grouse occurrence, explaining about 55% and 25% of the variation in hazel grouse occupancy, respectively. But, the effect of isolation was the second most important factor (about 10%), explaining a significant of the variation in hazel grouse occupancy of a habitat area in both areas. However, it did not occur as a measurement of distance. Instead, it occurred as a barrier effect at Aasla and to some extent also in Sala, with habitat areas surrounded mainly by forested land being more often occupied than habitat areas more surrounded by open land. This was expected, considering that the maximum distance between habitat areas in the small-scaled landscapes was only about one quarter of the critical threshold distance where isolation was found to exist in the intensively managed landscape (Papers III and IV). And, effects of distance-induced isolation effects have been suggested not to occur in landscapes with more than 30% remaining suitable habitat (Forman and Godron 1986, Andrén 1994, 1996). The barrier effect in Sala was also strengthen by an effect of landscape composition, with areas having a high proportion of clearcut within a radius of 800 m more seldom being occupied. Adding this factor to effect of size increased the proportion of explained variance of the model by an additional 10%.

The dynamics of hazel grouse occurrence in forested landscapes

Turnover, measured as appearance and disappearance of hazel grouse in habitat fragments (Paper IV) or habitat areas (Paper V) between seasons, was analysed in the intensively managed landscape and in the small-scaled landscape using multiple logistic regressions. I preferred to use appearance instead of colonization and disappearance instead of extinction, because in most cases in my study only one hazel grouse male either appeared or disappeared between two counts. Thus, I measured the turnover of individuals in territories (Haila 1990). The results were similar in the two landscapes and supported the results of hazel grouse occurrence stated previously.

The appearance of hazel grouse in habitat fragments during spring within the intensively managed forest (Paper IV) was mostly influenced by the amount of cover in the fragment, but second in importance was distance to nearest habitat fragment. In autumn, larger habitat fragments had a significantly higher probability of being occupied by hazel grouse than smaller habitat fragments. Distance to nearest suitable habitat fragment and the amount of cover also significantly influenced the probability of appearance during autumn. The influence of cover for occurrence of hazel grouse in habitat patches was also evident at the scale of home range (Paper II). Spring habitat had higher amounts of cover and a higher proportion of deciduous trees than autumn and non-habitat (Paper II, Table 1).

Habitat area was the dominating variable determining the appearance and disappearance of hazel grouse within the small-scaled managed landscape in spring (Paper V). The probability of appearance was significantly higher in large habitat fragments, whereas the probability of disappearance was significantly lower in larger habitat patches (Paper V). The importance of size was also evident in Paper IV, for the disappearance of hazel grouse during autumn in the intensively managed landscape. However, the appearance of hazel grouse in autumn within the small-scale managed landscape (Paper V) was mostly influenced by the type of vegetation surrounding the habitat area, with habitat areas surrounded by open land having fewer appearances.

Accuracy of model predictions

The occurrence of hazel grouse in the habitat patches at the Sala study area, some sixty kilometers northeast of Uppsala, (Paper VI) was predicted well using either the model developed with data from Kloten (Paper III) or with the model from Aasla (Paper VI), with 84% and 86%, respectively, of patches predicted correctly. The fit to the model developed at Aasla was very precise i.e. the slope of the regression line was close to 1 and the intercept close to 0 (Fig. 5).
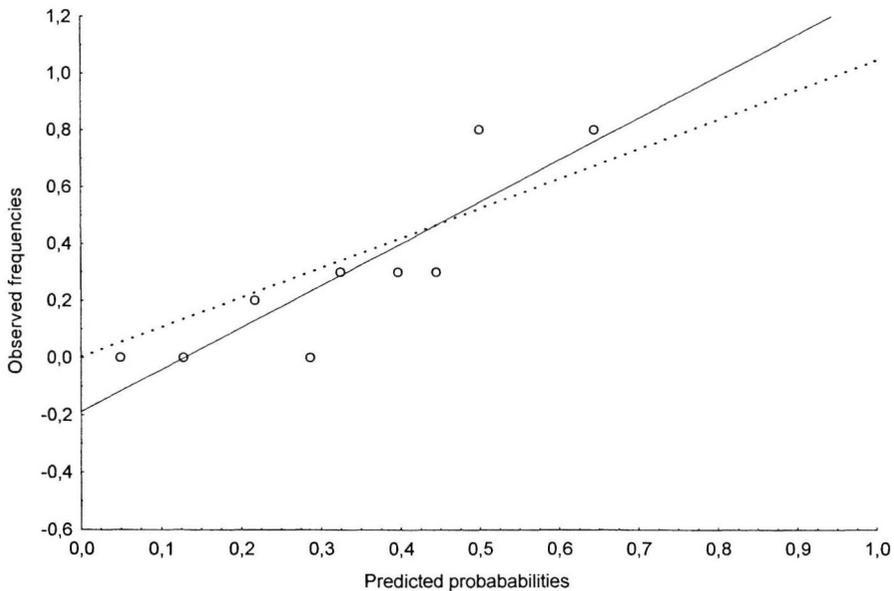
Figure 5. Relationship between predicted and observed occurrence of hazel grouse using the Aasla model in the habitat patches within the less intensively managed landscape near Sala some sixty kilometers northeast of Uppsala. The dotted line illustrates a perfect fit. (Paper VI).

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The fit to the Kloten model was statistically less precise i.e. the slope of the regression line, was significantly different from 1 and the intercept differed significantly from 0 (Fig. 6).
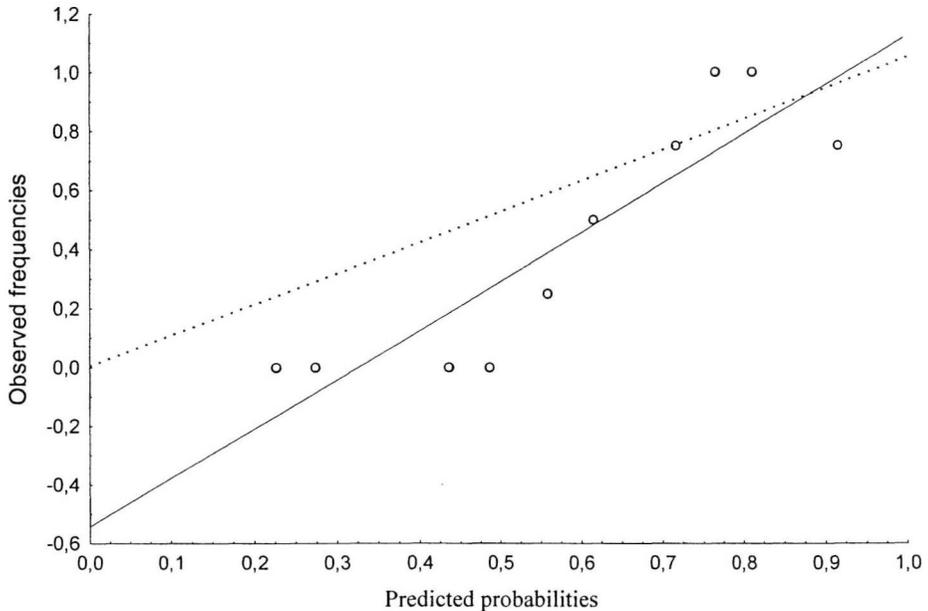

Figure 6. Relationship between predicted and observed occurrence of hazel grouse using the Kloten model in the habitat patches within the less intensively managed landscape near Sala some sixty kilometers northeast of Uppsala. The dotted line illustrates a perfect fit. (Paper VI).

Thus, the Aasla model predicted the occurrence of hazel grouse at Sala statistically very well, and better than the Kloten model did, which slightly overestimated the occurrence of hazel grouse. The difference in the two model predictions is important when applying the models in practical work. Probable reasons for the difference between the accuracy of the two models predictions were; differences in density of hazel grouse, different censusing techniques, the proportion of suitable habitat and open land differed between the studied landscapes, and possible effects of extrapolation. Choosing a species with specific narrow habitat requirements, whose habitat is well described, probably contributed to the successful modelling in this study. In addition good methods with known reliability to evaluate the occurrence of the species and the suitability of the habitat were available.

The proportion of correctly predicted presence and absence of hazel grouse in the patches within the intensively managed landscape near Grimsö Wildlife Research Station (Paper II) using the tree age and deciduous component criteria of Swenson & Angelstam (1993) separately, was 73 % and 55%, respectively (Table 2).

Table 2. Predicted and observed occurrence of hazel grouse in the 71 patches of managed forest using predictions based on Swenson & Angelstam (1993) study, regarding tree age, proportion of deciduous trees and combined. Predicted and observed absence of hazel grouse in a habitat patch is 0 and presence is 1. The proportion of correctly predicted habitat patches was 73%, 60% and 65%, respectively. (Paper II).

			Predicted			
	Age		Prop.decid. trees		Combined	
	0	1	0	1	0	1
	<20 yrs and >69 yrs	20-69 yrs	<1% and >20%	1-20%		
Observed						
0	35	9	30	14	37	7
1	10	17	14	13	18	9

When combining the two criteria, 65% of the patches was correctly predicted regarding the presence and absence of hazel grouse (Table 2). The accuracy of prediction of hazel grouse occurrence would, based on our study (Paper II), benefit if the model criteria for preferred hazel grouse habitat within managed forests were 5-40% deciduous trees and of an age of 20-69 years or older than 90 years. Moreover, the stands should preferably include alder, not be heavily thinned and the stands should have relatively rich vegetation with herbs and, preferably also *Vaccinium* species present (Paper 2).

Management implications
This thesis has several implications for the conservation of hazel grouse populations within a gradient of boreal landscapes that have been altered in different ways. Although suitable hazel grouse habitat is an absolute prerequisite for the existence of hazel grouse, this thesis has added the importance of some landscape ecological parameters. These parameters are; habitat size, type of matrix, isolation, amount of remaining suitable habitat in the landscape, and the

type of transition zone between hazel grouse habitat and non-habitat. For conserving hazel grouse, the habitat patches, i.e. the core area of habitat should, be larger than 10 ha in managed forested landscapes (Figs. 3, 4, 5 and 6). In landscapes where the habitat is situated in a matrix of non-forested habitat, areas of suitable habitat corresponding to the total home range area, i.e. 20-40 ha (Swenson 1991a) must be preserved (Paper III).

The distances over which hazel grouse disperse are strongly determined by the type of matrix in the landscape. Therefore habitat patches within intensively managed agricultural landscapes should not be separated by more than 100 m of open field, whereas the maximum inter-habitat distance within intensively managed forested landscapes should be about 2 km of non-habitat forest (Figs. 2 and 3). Also, hazel grouse habitat patches within less intensively managed and forested landscapes should be surrounded mostly by forested land (Papers V and VI).

The density of hazel grouse can be estimated during spring and autumn, using the method described and evaluated by Swenson (1991c). The prolonged study in the intensively managed and forested landscape (Paper IV) indicated the importance of several seasons of censusing before the effect of isolation on hazel grouse was clarified. Also important for conservation of hazel grouse was the study in the small-scaled landscape (Paper V), which showed that the correlation between habitat areas preferred by hazel grouse in spring or autumn and the presence of a brood in the habitat area in summer was high (Fig.7).
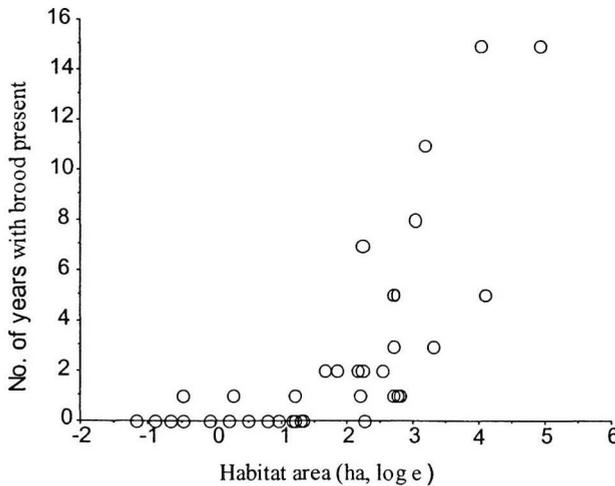

Fig. 7. Relationship between number of years (of 21) in which hazel grouse broods where present in the habitat patches and the size (ha, $\log_e$) of the habitat patches.

Thus, the presence of hazel grouse in a habitat area in spring, and autumn to some extension, can be used as a good indication of the suitability of a habitat area for reproduction. But, the best season to define suitable patches seems to be spring, based on the source-sink analysis (Paper II). However, using the whistling method as an instrument to identify small-scaled differences in hazel grouse habitat selection, caution must be considered regarding the heterogeneity or grain-size of the landscape (Paper I). The present forest stand descriptions do not give sufficient data to manage forest for viable hazel grouse populations and would benefit if measurements of cover, field-layer vegetation and alder were added.

In addition to horizontal stratification of habitats within the habitat patch (Papers II, IV), proportion of spruce and deciduous trees (Papers I and II), and presence of alder (Papers II and VI), several landscape features must be present (Papers III-VI), to conserve the hazel grouse in managed landscapes.

Conclusions

The preferred habitat of hazel grouse in managed boreal forests consists of non-thinned, middle-aged (or older than 90 yrs), rich deciduous stands dominated by spruce, but including alder, and with a rich field layer (Papers I, II). The spatial scale and degree of heterogeneity played a crucial role when examining the habitat selection of hazel grouse. Only a few clear patterns relating to hazel grouse habitat selection were found in spite of long-term data on a well-known species and detailed vegetation descriptions at spatial scales smaller than the species' home range (Paper I). The non-significant relationships were probable due to the generally suitable composition and small variation of habitats within the study area.

The effect of isolation occurred over much shorter distances when the surrounding habitat consisted of farmland than when it was intensively managed forest, which strongly suggests that the quality of matrix is an important factor influencing the dispersal abilities of hazel grouse (Papers III and IV). On the scale of territory size, the accessibility of a habitat area to hazel grouse was affected strongly by both the quality of the habitat directly surrounding the area (Papers V and VI) and by the composition of the entire landscape (Papers III-VI).

The size of the habitat fragments was important, with larger habitat fragments more often containing hazel grouse (Papers III-VI). Moreover, both the strong increase in the number of years with hazel grouse present in a habitat area and the number of years with a brood present in a habitat area occurred when patches exceeded about 10 ha in size (Paper V), suggesting that deciduous rich spruce areas at or larger than this size should be preserved. This pattern was also

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indicated in Papers III, IV and VI, and should be used as guideline if a goal is to conserve viable hazel grouse populations in managed forests.

The two regression models describing the occurrence of hazel grouse in the differently managed landscapes (Papers III and V) gave highly reliable predictions (>80% accuracy) when tested in a third landscape (Paper VI). Differences from the predicted were probably due to differences in amount of suitable habitat in the landscapes, but also indicate difficulties when applying knowledge received in one area into new one.

Thus, the hazel grouse appears to be very sensitive to habitat fragmentation and this thesis shows that to conserve hazel grouse, one must understand both the habitat requirements at the smaller scales, and the landscape ecological requirements.

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