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Species/habitat relationships and their responses at different scales are important aspects of ecological and conservational research. We studied the occurrence of hazel grouse *Bonasa bonasia* males in a forest reserve over a 10-year period at varying scales and population densities, using two sets of habitat descriptions. Avoidance of pine *Pinus sylvestris* was the only habitat effect in the hazel grouse/habitat analyses that was significant through all scales, seasons and densities. Thus, in spite of long-term data on a well-known species and detailed vegetation descriptions, only a few clear patterns relating to hazel grouse habitat selection were found at the relatively small scales analysed. We conclude that the non-significant relationships were due to the generally suitable composition and small variation of habitats within the study area, and that significant results may not be expected within the scales analysed and with the methods used. Thus, to find associations between animal species and habitats, a suitable study area must include a certain degree of habitat variation and the relationships should probably be examined at a scale equal to or larger than the home-range of the species in question, or considerably larger if population data are available. The results are discussed in relation to other studies and the applicability of the habitat descriptions and census techniques for conservation of hazel grouse populations in managed forests are discussed.

Key words: habitat selection, hazel grouse, heterogeneity, spatial scale, stochasticity

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Theories of habitat selection assume that individuals of a species occupy a restricted and favourable part of their potential habitats at low population density and thereby optimise their individual fitness (Wiens 1989, Rosenzweig 1991). The potential habitats are filled with territories in a deterministic order, often in a density-dependent fashion, as suggested by the models of Fretwell & Lucas (1969). Therefore, favourable habitats will more often be occupied than marginal habitats. In studies where the difference between the compared habitats is large, the modelled predictions often are realised quite well (O'Connor 1986, 1987). However, where the habitats are more similar and all are rather favourable, the spatial distribution of animals can be more stochastic (Rotenberry & Wiens 1980, Orians & Wittenberger 1991). The distribution of habitats in landscapes has been described as heterogeneous or homogeneous (Addicott, Aho, Antolin, Padilla, Richardson & Soluk 1987), a division clearly related to scale and the focal animals' ranges of movements (Forman & Godron 1986, Wiens 1989). A similar classification of landscapes is the separation between fine- and coarse-grained habitat patterns (Levins 1968), which by definition is related to the behaviour and landscape perception of the species under study.

The response of animals to the distribution of habitats has been shown to differ according to spatial scale (Rotenberry & Wiens 1980), in large-scaled studies due to the matrix (Åberg, Jansson, Swenson & Angelstam 1995, Saari, Åberg & Swenson 1998), as well as on the smaller scales due to habitat composition, e.g. within home-ranges (Jokimäki & Huhta 1996). Thus, multi-scale approaches in studies of animal/habitat relationships are of great importance (Wiens, Rotenberry & van Horn 1987).

The importance of stochastic versus deterministic factors in influencing the selection of territories by forest birds was studied by Haila, Nicholls, Hanski, & Raivio (1996). In their study of resident birds' territories over six years in a heterogeneous forest, an element of stochasticity was apparent. Haila et al. (1996) found that avoidance of certain areas by birds was predictable, whereas a specific habitat preference was not. They concluded that, in relatively suitable areas, individual birds might not seek to optimise their territory but rather to find an acceptable one, and that the influence of stochastic events must be evaluated at several spatial scales.

We have studied the habitat selection of the hazel grouse *Bonasa bonasia*, which is considered to be a habitat specialist (Eiberle & Koch 1975, Scherzinger 1979, Swenson & Danielsen 1991, Swenson & Angelstam 1993), in a forest reserve. In this paper we examine the role of stochasticity on habitat selection on several spatial scales using a 10-year data set. Two types of digitised vegetation data were used; firstly, a detailed vegetation description obtained especially for hazel grouse and this study, and secondly, the common forestry maps of the study area. The study aimed to answer two questions: 1) are stochastic or deterministic factors more important in habitat selection in a generally good environment, and 2) how does the spatial scale of measurement influence the observed pattern of habitat selection? Also, we discuss methodological problems in measuring habitat selection to predict the occurrence of the species, and to evaluate the applicability of forest stand descriptions and census techniques for the management of the species.

Study area

The study area covers 522 ha and is located in south-central Sweden (59-60°N, 15-16°E). Forest dominates the area (72%), but bogs are also common (18 %; Cederlund 1981). In 1914 most of the forest in the study area was burned, but between 1914 and 1972 modern intensive forestry was conducted. After 1972, the forestry activities ceased, and the area became a nature reserve in 1993. The western part of the study area (Fig. 1) was dominated by Norway spruce *Picea abies* (57% of trees), white birch *Betula pendula* and pubescent birch *B. pubescens* (together 22%), and Scots pine *Pinus sylvestris* (17%). Other deciduous trees (4%) included aspen *Populus tremula*, black

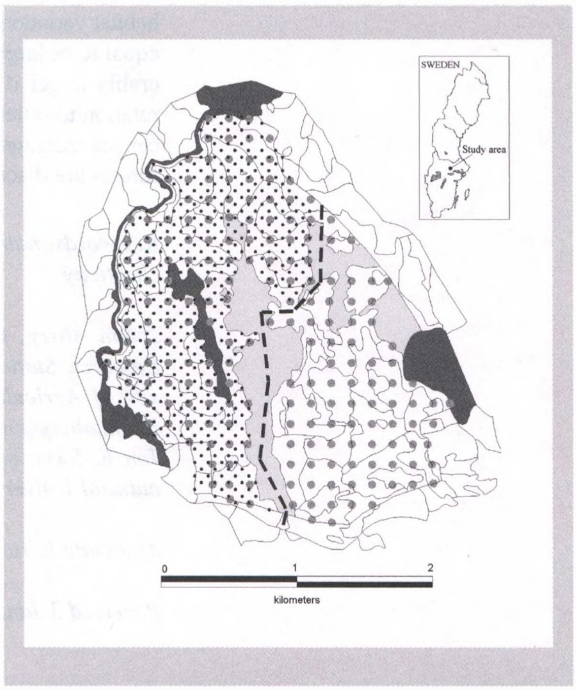

Figure 1. The forest reserve and immediate surroundings with indication of the study area. Grey circles represent the 197 hazel grouse census points and black dots the sampling plots on which the detailed vegetation description was performed. Thin lines define the different forest stands. Dark grey areas are lakes and lighter grey areas are bogs. The dotted line in bold divides the western from the eastern part of the forest reserve.

alder *Alnus glutinosa*, goat willow *Salix caprea*, rowan *Sorbus aucuparia* and grey alder *A. incana*. The eastern part had a much lower proportion of deciduous trees (Swenson 1991b), but spruce was still the dominating coniferous species. The proportion of deciduous trees in the stands surrounding the reserve was very low, < 7% (Anon. 1999:66) and in stands more than 60 years old the deciduous component was < 1% (Swenson & Angelstam 1993). The field layer throughout the reserve was dominated by bilberry *Vaccinium myrtillus*, cowberry *V. vitis-idaea*, and wavy hairgrass *Deschampsia flexuosa*.

Methods

Forestry stand descriptions

The former owner of the reserve, the Swedish National Forest Enterprise (SNFE), supplied data on all stands producing at least 1 m^3 timber/ha/year in the reserve, and also on the stands surrounding the reserve. Less productive areas were classified into bogs, rocky outcrops, lakes and fields. The following habitat data were listed in the descriptions: the mean age of each stand, the proportion of different tree species in the stand measured using basal area, standing volume, moistness, topography, productivity and the proposed forestry measures to be conducted. The last four habitat variables were listed as categories in the descriptions. The maps and descriptions were produced in 1993, using the standard methods in operational forestry in Sweden as described by The Swedish National Board of Forestry (Anon. 1988). The map was digitised and the habitat data on the stands accompanying it were linked into a Geographic Information System (GIS) for the present study.

Detailed vegetation data

Fine-scale habitat data were collected in the western part of the area during summer 1988, for another study on hazel grouse (Danielsen 1990). The sampling plots were placed systematically at each node and at the midpoint of a 100 x 100 metre grid, for an overall density of two plots per ha (see Fig. 1). Each plot encompassed a circle with a 10-m radius. Plots located more than 50 m into bogs or open fields were not described, because hazel grouse avoid open areas (Swenson 1993a). The variables measured or estimated in the plots were based on forest grouse studies by Marcström, Brittas & Engren (1983) and included:

1) measured height of canopy in metres and density of canopy cover estimated to the nearest 10%;
2) coverage of spruce (defined as trees > 3 m) and total coverage of shrubs (defined as trees < 3 m) estimated to the nearest 10%;
3) estimation of the horizontal cover of the plot from the four cardinal directions at a distance of 15 m using a cover board (Nudds 1997). The covered proportion of a 0.5 x 0.4 metre rectangle was estimated from each direction into one of six categories: 0 = 0%, 1 = 1-20%, 2 = 21-40%, 3 = 41-60%, 4 = 61-80%, 5 = 81-99% and 6 = 100%. These values were summed for each of five height intervals, from 0-0.5 m to 2.0-2.5 m. The total horizontal cover was defined as the sum of values for each rectangle;
4) density of the field layer plant species, assumed to be important ingredients of hazel grouse diet (Ivanter 1962, Ahnlund & Helander 1975, Eiberle & Koch 1975, Wiesner, Bergman, Klaus & Müller 1977) estimated to the nearest 10%. These species were *Vaccinum myrtillus*, *V. vitis-idaea*, *Eriophorum* spp., *Viola* spp., *Anemone nemorosa*, *Oxalis acetosella* and *Potentilla erecta*;
5) tree species composition and standing volume of trees higher than 3 m, measured using a relascope (Bitterlich 1984);
6) type of soil (thee classes), presence of rock (three classes), and moisture of the ground (three classes) were estimated.

These data, in total 76 habitat variables, were linked to the forest stand map as a second layer in GIS.

The studied species

The hazel grouse is dependent upon spruce-dominated multi-layered forests with a deciduous feature, preferably alder (Swenson 1993b). The species is sedentary and territorial, shows low dispersal ability (Swenson 1991a, Swenson & Danielsen 1995) and is sensitive to habitat isolation (Åberg et al. 1995, Åberg, Swenson & Andrén 2000, Saari et al. 1998), which all together makes it an appropriate species for studies of its habitat dependence (Beshkarev, Swenson, Angelstam, Andrén & Blagovidov 1994, Jansson & Angelstam 1999). That is, the biology of the species is relatively well understood (Bergmann, Klaus, Müller, Scherzinger, Swenson & Wiesner 1996).

Censuses of hazel grouse

The forest reserve was censused for hazel grouse males in autumn 1987, and spring and autumn 1988-1997;

however, in spring 1988 only the western part was censused. Censusing was conducted at a total of 197 points placed at 150-m intervals (see Fig. 1), and visited once per season between 15 April and 15 May in spring and between 15 September and 15 October in autumn. The males' territorial song was imitated for six minutes at a rate of two signals per minute from these points, using a hunting whistle. The method used, described by Swenson (1991c), discovers > 82% of all territorial males within 100 m, as determined from tests using radio-marked birds in the study area. The distance covered by the census method exceeded the distance between the census points. This introduces an element of risk of counting the same bird twice, which would result in an incorrect density. However, individual hazel grouse differ somewhat in their responses, i.e. vocalisation and behaviour (Bergmann et al. 1996), and it is therefore possible to separate individuals at adjacent census points. The field map used during censuses was a cross-country map (1:15,000) with a very high resolution showing trails, larger boulders and signs of former charcoal burning sites. All 197 census points were digitised as a third layer on the forest stand map, as were the hazel grouse occurrence data for the study period.

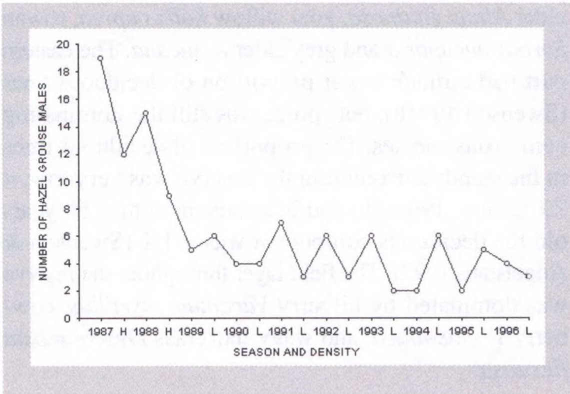

Figure 2. Number of male hazel grouse found in the study area per season. Years on the x-axis denote the autumn and unlabeled ticks the spring for the respective year. Each season (autumn-spring) is defined as showing either high (H) or low (L) density based on the mean number of males in autumn year 1 and in spring year 2.

Statistical analysis

The SNFE forest stand descriptions were used to analyse the habitat selection of hazel grouse males using the vegetation parameters of the stand. A correlation matrix was formed for the original 12 parameters measured. As several of the parameters were correlated, a principal component analysis (with the varimax rotation normalised; see Statistica 1997) was performed to reduce the number of habitat variables and the correlation among the four continuous variables. By this method the habitat variables were reduced to two independent habitat variables (Appendix I). These variables were related to coniferous and deciduous forests, respectively. The coniferous component was negatively correlated to pine and positively correlated to spruce, and the deciduous component was positively correlated to deciduous trees. A reduced number of habitat variables (PC-scores <0.1) were incorporated in the PCA-components. The number of male hazel grouse occurrences at each census point, which could vary within 0-20 for all seasons combined, was summarised, as were the number of hazel grouse occurrences separately during spring and autumn. Moreover, the first four seasons (autumn 1987 - spring 1989) were defined as seasons of high density (Fig. 2). Multiple stepwise regression was used to analyse the influence of the habitat variables at the census point on the number of times male hazel grouse were present during each period. Also, multiple logistic regression was used to analyse the effect of habitat on the presence or absence of hazel grouse at a census point for the different periods.

The range of the census method (75 m) was used to define step one in the scale analyses. Thereafter a factor of 1.5 was used to create the other steps, which were 33, 50, 112 and 169 m. Thus, the largest area analysed (radius 169 m) using the detailed vegetation material constituted approximately half a normal hazel grouse male home-range in the study area (Swenson 1991b). The vegetation for each census plot was described using the detailed vegetation data for the five spatial scales. At the smallest scale, only one vegetation point was used per census plot, whereas at the scale of 50 m most often two vegetation plots fell within the range, and on the scale of 75 m four vegetation plots usually fell within the range and so on. When more than one vegetation point was within the radius, the mean of the vegetation parameters was used. Thus, some of the vegetation variables were common for some census points, especially on the larger scales. Variables indicating structures of very low abundance or not normally distributed were excluded from the analysis. As several of the parameters were correlated, a principal component analysis (with the varimax rotation normalised; see Statistica 1997) was used to reduce the number of habitat variables and the correlation among them. Of the original 76 habitat variables, several variables were measured as categories, such as type of soil, or were too rare (mostly field layer species) to use in a PCA. No classes of variables were left out. Thus, 15 variables were used in the PCA where four independent habitat components were left (Appendix II). The new habitat components created were mainly the same at all scales, but the relative importance differed between scales. The components were interpreted as follows: 1) 'Cover', constituting the horizontal cover at several heights, 2) 'Coniferous', constituting pine and spruce, 3) 'Age', constituting tree height, canopy cover and standing volume, and finally 4) 'Shrubiness', constituting moisture and shrub cover. Only variables with PC-scores <0.1 were incorporated in the PCA-components in order to reduce the number of habitat variables. In an additional analysis, the original variables were grouped into four groups, based on the relationships among the original variables. The groups were cover, tree species composition, field layer and finally a group with variables being related to tree age. For each of these groups, a PCA was performed which resulted in one principal component for each of the groups. There are, of course, difficulties in grouping the variables correctly, because most of the parameters are very correlated by nature, and the earlier impacts of forestry practises in the area, but grouping was done to obtain a greater descriptive power in the analysis. Multiple stepwise regression was used to analyse the influence of vegetation parameters on the number of times a male hazel grouse was present at a census point. Absence or presence of hazel grouse during both seasons, springs and autumns, and during low and high densities was analysed using a stepwise multiple logistic regression.

To visualise the occurrence pattern of hazel grouse males over the study period, a 20-ha grid was imposed on the study area (i.e. the whole reserve), with a grid cell size similar to hazel grouse territories in the study area, i.e. 15-25 ha (Swenson 1991b). That is, in this analysis, the occurrence per grid and season was normally based on nine census points. However, as no censusing was performed on bogs or lakes (see Detailed vegetation data) and due to the shape of the reserve, the number of census points varied. Therefore the dependent variable, the number of male hazel grouse occurrences in a grid per season for all seasons (21) and all years (10) were divided by the number of censused points in each grid. The characteristics of the grid cells were described using the mean of the forest stand description variables (stand age, proportion of pine, spruce and deciduous trees) for each census point in each grid, respectively, transformed into PCA-variables for each grid. The relationship between the number of occurrences of hazel grouse in a grid cell and the PCA-variables were analysed, as were the original habitat variables, using multiple regression.

Results

Using the forest stand descriptions, no single habitat variable measured in this study was significantly re-

Table 1. Habitat variables included in the multiple logistic regressions having a significant (P < 0.05) effect in explaining the occurrence of hazel grouse in the entire study area (172 census plots), and in the western (108 census plots) and eastern area (64 census plots) separately, based on the forest stand descriptions.

	Multiple logistic regression		
Dependent variable	Entire reserve	Western part	Eastern part
Spring and autumn	Coniferous	-	Coniferous
Constant	-0.42	-	1.78
G, df	9.76, 1		5.68, 1
P	0.0018		0.015
Spring	-	-	-
Autumn	Coniferous	-	-
Constant	-1.03		
G, df	15.02, 1		
P	0.0001		
High density	Coniferous	-	Coniferous
Constant	-1.45		-2.41
G, df	15.50, 1		4.81, 1
P	0.0001		0.026
Low density	Coniferous	-	Coniferous
Constant	-1.04		-2.06
G, df	4.85, 1		5.35, 1
P	0.028		0.019

lated to the occurrence of hazel grouse in the western part of the study area during spring, autumn, combined seasons nor periods of high or low hazel grouse density (Table 1). However, the coniferous component was significantly and negatively related to the occurrence of hazel grouse in the eastern part during spring and autumn combined, and in years of high and low hazel grouse density. This was presumably due to the fact that the PCA-component coniferous forest was composed of both pine and spruce, and an increasing proportion of pine negatively influenced the occurrence of male hazel grouse. Also for the entire reserve, a significant effect of coniferous forest was found for the occurrence of hazel grouse during autumn, combined seasons, and years of high and low hazel grouse density (see Table 1). Moreover, the total number of hazel grouse occurrences was negatively related to an increasing amount of coniferous forest in the eastern ($P = 0.015$) and entire reserve ($P = 0.0003$), but no habitat variable was significantly related to the number of hazel grouse occurrences in the western area using the stand descriptions. The original tree species variables incorporated in the principal components coniferous and deciduous for the entire reserve, the western and the eastern part are presented in Appendix III. Analysing the original habitat variables separately using multiple regression showed that the proportion of spruce was significantly and positively related to the occurrence of hazel grouse in the eastern part during all seasons, during low density and during high density (all Ps < 0.01).

When analysing the ungrouped detailed vegetation data and the occurrence of hazel grouse during spring, autumn, combined seasons, and years of high or low hazel grouse density, we found that shrubiness was significantly and positively ($P = 0.025$) related to the occurrence of hazel grouse during autumn at the largest scale (169 m) in the western part. The number of hazel grouse occurrences was significantly and negatively ($P = 0.017$) related to an increasing amount of pine at the smallest scale (33 m). The grouped principal components of the detailed vegetation data, analysed in the same way as the ungrouped, showed one significant relationship. That was a positive relationship between the number of hazel grouse occurrences at a census point and the proportion of field layer ($P = 0.04$) at the scale of 112 m.

The number of occurrences of hazel grouse males within the grid cells varied within 0-12 during the study period (Fig. 3). A significant relationship was found between the number of hazel grouse occurrences in a grid cell during all seasons and during low and high density using the forest stand description. The significant relationship was found for both the PCA-variable coniferous forest (negative) and the original habitat variable spruce (positive) on number of hazel grouse occurrences (all Ps > 0.01; Table 2).

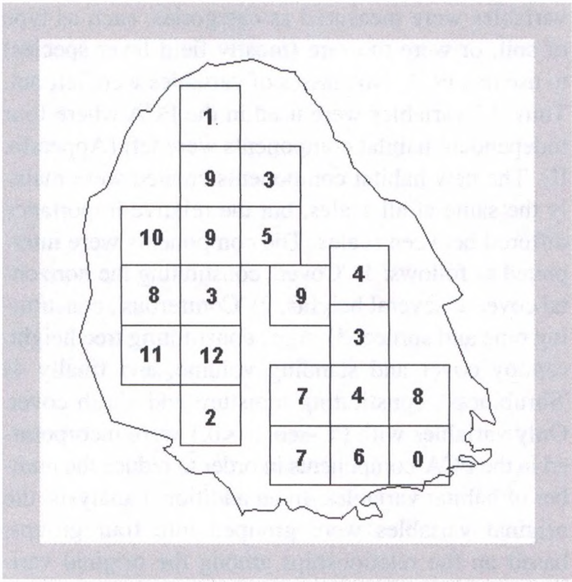

Figure 3. Location of the grid cells in the forest reserve showing the number of hazel grouse presences in each grid cell during the study period.

Discussion

We used a 10-year data set of hazel grouse censuses,

Table 2. Habitat variables included in the multiple regression having a significant ($P < 0.05$) effect in explaining the occurrence of hazel grouse in the 20 grid cells, based on the forest stand descriptions.

	Multiple regression	
Dependent variable	PCA-variable	Original habitat variable
Spring and autumn	Coniferous	Spruce
Constant	-0.31	1.34
F, df	15.53, 19	27.3, 19
P	0.0025	0.0001
Spring	-	-
Autumn	-	-
High density	Coniferous	Spruce
Constant	-1.11	3.21
F, df	11.50, 19	31.45, 19
P	0.0061	0.0001
Low density	Coniferous	Spruce
Constant	-1.25	2.1
F, df	12.61, 19	22.65, 19
P	0.0093	0.003

collected using an inventory method with a high and known reliability, over a large area for which the habitat composition was carefully described. Yet, despite this, no clear relationships between the occurrence of hazel grouse males and the parameters of vegetation measured were found at any of the spatial scales analysed in the western part of the study area. One may have expected hazel grouse male occurrence to be influenced by habitat parameters such as tree species composition or tree age, as the hazel grouse has been considered to be a habitat specialist (Swenson & Danielsen 1991, Swenson & Angelstam 1993, Wiens 1989). Furthermore, the hazel grouse has been shown to recognise differences between source and sink habitats in natural forests (Beshkarev et al. 1994), as well as in a managed-forest dominated landscape (Lindén & Wikman 1983). However, our study area constituted only a small portion of the landscape where Swenson & Angelstam (1993) performed their study. We suggest that the range of habitat variation in our study area was apparently too small to produce any clear patterns for habitat or patch preferences of hazel grouse males at the smaller scales studied and methods used. Instead of preferences, the only significant relationship we found was the negative influence of the PCA-component 'coniferous'. This was probably because one variable of that component was the number of pine trees, and pine-dominated habitats are rarely used by hazel grouse (Swenson 1993a).

The results of our study are comparable to those of Haila et al. (1996) in several aspects. In contrast to our study, Haila et al. (1996) used a rather small study area (36 ha) and included fairly generalised species in their study, for which some of the home ranges probably were as large or larger than the whole study area. Further, they analysed species occurrences in relation to habitat variables measured around the nest, even though the position of the nest may not be in the most typical or preferred part of the home range, as they mention themselves. Therefore, it may not be surprising that they did not find any clear preferences for habitat selection by the studied species. However, in spite of our long-term data on a specialist species and detailed habitat descriptions covering a study area that was more than 25 times larger than the average home range of a hazel grouse, we found neither clear preferences for specific habitat types nor structures. Instead, the avoidance of a certain habitat (the PCA-component 'coniferous') by the hazel grouse was predictable, which is similar to what Haila et al. (1996) found for some species. The occurrence of hazel grouse males was better explained in autumn than in spring. An increasing amount of cover and a decreasing percentage of pine positively influenced the occurrence of hazel grouse during autumn, a pattern in agreement with what Åberg et al. (2000) reported from a nearby intensively managed forest area, measured on a landscape level. We propose that the general lack of relationships was due to the following factors:

1) the habitat composition in general was probably suitable or acceptable (*sensu* Haila et al. 1996) for the hazel grouse throughout the study area, in particular in the western part. That is, the qualitative differences among 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 scales analysed, as a) >10 census points fit within a normal hazel grouse male territory, and the point at which a male was observed in a given season, may therefore be coincidental, and b) several vegetation points were in common for some census points, which may have diminished the differences and the effects of the habitat at the site at the larger scales;
3) although the scales considered (33-169 m radii) were large relative to the number of vegetation points included, these distances are quite small relative to hazel grouse territories. We conclude that within an area composed of generally suitable habitats for the focal species, and at scales smaller than its home range, clear patterns of habitat preferences may perhaps not be expected.

The importance of the proper spatial scale for studying the habitat selection of the hazel grouse, measured as presence or absence at a census point, is obvious. At the larger scales, several vegetation points were common for some census points, which may have diminished the differences in habitat structure for the census points at the larger scales, resulting in a low level of explanation. And, at the smallest scale the vegetation points may have been located at random in a fine-grained landscape, resulting in weak relationships. On the other hand, the occurrence of hazel grouse has been shown to be independent of scale regarding the presence of alder, which was important for hazel grouse at the four measured scales (Swenson 1993b). In a study of breeding birds in an urban landscape in southern California, the landscape ecological parameters at larger scales were found to predict the occurrence of some species better than the fine-scaled parameters (Bolger, Scott & Rotenberry 1997). In our study, the occurrence of hazel grouse was explained better at the largest scale, i.e. the eastern part of the forest reserve compared to the western part. This was expected because the proportion of hazel grouse habitat was considerably lower in the eastern part and because the difference between good and bad habitat was more distinct (Kareiva 1990). However, the total number of hazel grouse occurrences at a census plot was significantly influenced only by the habitat variables at our smallest scale, a scale where Haila et al. (1996) found bird abundance to be most linked to the heterogeneity of the habitat.

The overall density of hazel grouse (low and high) did not influence the predictability of hazel grouse occurrence in the western area, as opposed to the eastern more heterogeneous part, where the occurrence of hazel grouse was more predictable during years of low densities. The amplitude of the density variation, or the difference between low and high years, was perhaps too small to detect an effect in the more rich western area. The analysis of the grid cells, perhaps questionable due to the low N-value, showed no statistical relationship between the number of hazel grouse occurrences and the quality of the habitat. It is probable that some subtle habitat parameters that we did not measure, or did not measure adequately, in addition to habitat heterogeneity and stochasticity, were important in influencing this pattern of grid occupancy. Moreover, as the methodology in this study only considers the occurrence of hazel grouse males, the occurrence of males can be influenced by the distribution of hazel grouse females.

Our results suggest that at least the scale of territory size is a proper level to investigate possible patterns of density dependent habitat selection in a species. At smaller scales, i.e. within territories or home ranges, the occurrence of individuals is more stochastic. For example, in the extreme case of a certain 1-m^2 plot, the probability of the presence of an individual such as hazel grouse is always very low regardless of habitat. Therefore, to find associations between animal species and habitats, a suitable study area must include enough habitat variation and the relationships should probably be examined at a scale equal to or larger than the home range of the species in question, or considerably larger if population data are available.

Ecologists commonly agree that for an effective promotion of biodiversity in forests, there is a need for methods and measurements applicable in management (Harris 1984, Noss 1990, Angelstam 1997, Jansson & Angelstam 1999), as well as knowledge of the relevant spatial and temporal scales (MacArthur & Wilson 1967, Wiens 1976, 1989). The whistle census method seems to be suitable to estimate densities and the presence or absence of hazel grouse males in a certain area (Swenson 1991c). However, as an instrument to analyse small-scaled differences in hazel grouse habitat selection, caution must be taken regarding the heterogeneity or grain-size of the landscape. In this respect, telemetry is probably a better method, unless a repeated number of visits using the whistle at a census plot are conducted and the fact that birds may leave their original position and approach the whistler is taken into consideration. The forest stand descriptions we used did not give sufficient data to manage the forest for viable hazel grouse populations in this area, although a high proportion of pine negatively influence the presence of hazel grouse. In addition to horizontal stratification of habitats within stands, which has been shown to be important for the hazel grouse (Swenson & Angelstam 1993), there is also a substantial need for a landscape perspective in forestry planning, to preserve the hazel grouse in managed landscapes (Åberg et al. 1995, Saari et al. 1998, Åberg et al. 2000).

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Appendix I

Principal component loadings for the four original continuous habitat variables using the forest stand descriptions for the entire area, the western area and the eastern area. The principal components have been rotated with the varimax normalised (Statistica 1997). Percentage explained refers to the percentage of the total variance explained by the rotated components and the loadings marked in italics are > 0.7000.

Entire area (N = 176)		
Component	1	2
Name	Coniferous	Deciduous
Percentage explained	42.6	36.3
Age	0.10258	0.59819
Pine	*-0.91325*	0.39799
Spruce	*0.88699*	0.38950
Deciduous	0.15650	*0.91291*
Western area (N = 112)		
Component	1	2
Name	Coniferous	Deciduous
Percentage explained	41.7	38.4
Age	0.10258	0.64487
Pine	*-0.99609*	0.08488
Spruce	0.60261	0.53190
Deciduous	0.52377	*0.78613*
Eastern area (N = 64)		
Component	1	2
Name	Coniferous	Deciduous
Percentage explained	47.3	32.6
Age	0.24436	0.62725
Pine	*-0.82622*	0.47538
Spruce	*0.97927*	0.15075
Deciduous	0.14628	*0.91141*

Appendix II

Principal component loadings for the 15 original continuous habitat variables using the detailed vegetation description for the western area at the largest scale area (N = 119). The principal components have been rotated with the varimax normalised (Statistica 1997). Percentage explained refers to the percentage of the total variance explained by the rotated components and the loadings marked in italics are > 0.7000.

Component number	1	2	3	4
Name	Horizontal cover	Pine	Age	Shrubiness
Percentage explained	45.9	13.8	12.4	9.0
Moisture	-0.40911	0.12832	-0.18045	*-0.75852*
Shrubs cover	0.01316	-0.1524	0.04806	*-0.92169*
Canopy cover	0.50048	0.69529	0.05192	0.09991
Basal area	0.09868	*0.78196*	*0.25921*	0.05122
Tree height	-0.10292	0.01624	*0.81409*	-0.21926
Pine, %	0.20137	*-0.76061*	0.19199	0.04654
Spruce, %	0.1755	0.35366	*0.72717*	0.26224
Birch, %	-0.28092	0.30981	-0.68141	-0.40117
Cover top	*0.91246*	0.12301	0.02087	0.19647
Cover top-medium	*0.93471*	0.10794	0.05176	0.18631
Cover medium	*0.96317*	0.04483	0.06143	0.06999
Cover medium-bottom	*0.9461*	0.01509	0.06079	0.06398
Cover bottom	*0.77551*	-0.21965	0.01766	-0.08127
Cover total	*0.98504*	0.03391	0.06914	0.11279
Cover spruce	*0.75091*	0.20495	0.24602	0.34471

Appendix III

Mean and standard variation of the original variables originating from the detailed vegetation description, incorporated in the principal components pine and moistness at the five different spatial scales.

	Habitat variable		
Area	Pine	Spruce	Deciduous
Entire			
Mean	35.1	47.1	17.8
Standard variation	2.6	2.3	2.1
Western			
Mean	31.4	48.9	19.6
Standard variation	2.5	2.1	2.3
Eastern			
Mean	41.8	46.1	12.1
Standard variation	2.7	2.6	1.8