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David Jenkins
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Udine, Italy, 20-24 September 1993

WORLD PHEASANT ASSOCIATION

Proceedings of the 6th International Symposium on Grouse

20-24 September, Udine, Italy

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WPA was established in 1975 and is now the umbrella organisation for the five Galliform Specialist Groups of BirdLife International and IUCN. These cover pheasants, grouse, cracids, megapodes and partridge, quail and francolin.

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EDITOR'S PREFACE

Previous symposia on grouse organised by the World Pheasant Association have begged the question of the origins and aims of the WPA, and of the objectives of these symposia on grouse biology. Few participants at these symposia know what WPA is. Originally, the Association was a group of six British enthusiasts who decided in 1975 that there was a need for an organisation to advise world conservationists on problems concerning galliforms. As it happened, these six people were aviculturists, former members of the Pheasant Trust.

Because of their origins as aviculturalists and because they were mostly in business, they were well placed to encourage pheasant conservation, initially primarily geared to aviculture, in groups of people among whom professional conservationists had little contact. No founder member of the Association was a wildlife biologist. But these initiators of specialist galliform conservation soon found that they were entering a field dominated by scientists, among whom they remained well-informed amateurs. So they enlisted the aid of specialists, particularly for conservation activities, and they introduced a strategy for aviculture based on modern scientific concepts.

In Britain, these specialists included university biologists and staff of the Game Conservancy and of the Nature Conservancy, soon to become the Nature Conservancy Council and the Institute of Terrestrial Ecology. Scientists from these organizations were enlisted to help the infant WPA and to form a scientific advisory committee to advise WPA's Council. For geographical reasons, the founder members initially concerned themselves with pheasants in Asia (Howmans), with grouse in Europe (Lovels) and with the New World (Grahames). Developments in these areas have proceeded at different rates. The New World rapidly developed its own impetus, initiating WPA -North America and -South America as separate entities, the latter initially expanding under the aegis of the NYZS. Both North and South American initiatives are now progressing solidly. Specialist groups eventually evolved covering all galliform taxa. Howman is now the Director General of the Association.

In Asia, the entrepreneurial and business skills of Howman have added greatly to the development of pheasant conservation, providing a model for bird conservation working jointly with ICBP/BirdLife International and with IUCN, leading to the creation of pheasant 'chapters' in five (soon to be seven) countries and no fewer than five triennial symposia. Grouse lag not far behind with one more symposium and with local national WPA groups in France, Germany and Benelux. Under Lovel, grouse biologists, like those working on pheasants and the other galliform taxa, have organised a specialist group jointly with BirdLife International. The main task of specialist groups is to promote action for the conservation of defined endangered species, as a basis for a Conservation Strategy.

The standard of the symposium volumes has varied considerably. Latterly, published proceedings of symposia have become increasingly professional with the aim of attracting scientists who require critical organisation and editing. These symposia are now organised with peer referreeing of papers taking place during the course of each meeting, and the production of this particular volume has required WPA to purchase new sophisticated software for desktop publication, with most of the work done by Howman's secretary.

The aim is to attract to symposia a mixed-age group of scientists from many countries to meet each other and talk informally, to exchange information and to publish their results, some at early stages of investigation and some advanced. There are many other outlets for publication of scientific papers on grouse, in several languages and in several countries. The proceedings of the grouse symposia do not compete with these. Rather they offer both experienced mature scientists and young biologists beginning their careers an opportunity for sympathetic and critical discussions and refereed editing of their papers, at whatever stage of the results, and quick publication in a responsible journal.

Readers of this volume will make their own judgement of the success of this aim. The journal carries papers of wide interest, from the solitary displaying Black Grouse of the Italian alps to a 40-year study of Capercaillie in northern Russia, through several papers on the biology and management of Hazel Grouse and Black Grouse, to abstracts of a variety of papers at earlier stages of completion. All have been edited critically. Longer papers have all been refereed. All WPA symposium volumes on grouse, pheasants, partridges (+ quail and francolin), cracids and megapodes are on an evolutionary curve, aiming at improvement which, in the case of grouse, will be maintained or increased at Fort Collins in 1996. The founders of WPA who met in 1975 were imaginative people. It is now for the scientists who meet together two decades later to realise this imagination, and to come to WPA symposia with new ideas and to discuss them and contribute to the next post-symposium volume of proceedings.

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26.4.94

Population dynamics

Populations and habitats of snowshoe hares, Ruffed and Spruce Grouse in the southern boreal pine forest of Ontario

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Introduction

Our objectives were 1) to determine the abundance and patterns of change in the abundance of hares and grouse in different but nearby habitats, 2) to discover whether changes in the abundances of the three species were correlated, and 3) to evaluate as far as possible the impacts of cover, food supply and predation on populations.

Despite the ecological, economic, and aesthetic importance of snowshoe hare *Lepus americanus,* Ruffed *Bonasa umbellus* and Spruce Grouse *Dendragapus canadensis,* this is the only long term population study of the three species in the southern boreal forest of Ontario. Moreover, we attempt to compare the population dynamics of these species in the same and different nearby habitats. The comparative method is a powerful way of revealing factors possibly controlling abundance and how species may be linked to each other and their habitats. The three species are non-migratory, mainly herbivorous, about the same size and mass, largely sympatric in distribution, and share the burden of almost the same predators. Snowshoe hares feed heavily on plants that are food or produce insects that are food of both grouse (Bump et al. 1947, de Franceschi and Boag 1991, Dodds 1987, Radvanyi 1987). Food supply, competition for food, and the impacts of predation seem factors likely to affect populations of the three species either directly or indirectly and individually or together.

Boag and Schroeder (1992) suggest that populations of Spruce Grouse fluctuate primarily in response to post-fire regrowth of lodgepole *Pinus contorta* or jack pine *P. banksiana* forests and secondarily to predation. Bendell and Szuba (1993) show the remarkable stability and abundance of populations of Spruce Grouse over at least seven years. Boag and Schroeder (1992) and Szuba and Bendell (1983) also relate level of breeding density negatively to the age of jack pine forest. Population regulation about a particular level of density is apparently caused by the spacing behaviour of females in relation to the foods required for reproduction (Naylor and Bendell 1989, Naylor 1989). Both Ruffed Grouse and hares are most abundant in the thicket or early successional stage of deciduous and mixed conifer deciduous forest (Gullion 1984, Radvanyi 1987). Hares avoid habitats with less than 60% conifer foliage cover at 1-3 m above ground (Radvanyi 1987).

Hickey (1955) reviewed the American literature on population research on gallinaceous birds including the 10 and 3.5 year cycles attributed to species of grouse. In Ontario, populations of both Ruffed Grouse (Clarke 1936) and snowshoe hare (MacLulich 1937) showed cyclic fluctuations with a periodicity of 9-10 years. Keith (1963) emphasized the ten-year cycle in some populations of hares and of Ruffed Grouse, and considered the Spruce Grouse in some areas to show a similar cycle. Recently, Keith and Rusch (1986) augmented the relatively large literature on Ruffed Grouse and snowshoe hare and concluded that the 10-year cycle of the hare was linked to that in Ruffed Grouse. When hares declined, their predators switched to and caused the decline of grouse. Keith (1979) suggested that increase of hares was caused by the abundance of food while the decline was the result of food shortage and predation. Bergerud (1988) states that grouse generally are never short of food and that predation regulates their density. In brief, populations of grouse and hares may be cyclical, fluctuate, or stable. Explanations for populational change include stage of forest growth, the food supply, and predation. Populations of hares and Ruffed Grouse may be linked by the switch of predators from hares to grouse.

Study areas

Grouse, hares and their habitats were studied all or in part from 1979 to 1994 within an area of c. 1,200 km^2 north and south of highway 560 and immediately east of highway 144 (Fig. 1). The juncture of highways is 32 km south of the village of Gogama which is at 47° 30' N, 81° 40' W. The study area was within the Chapleau Plains Ecoregion (Wickware and Rubec 1989) and contained jack pine forests on lowland flat deep sands, and mixed conifer deciduous forests on the slight and rolling upland of rock and sandy soils. The region has been cut, burned and reforested since about 1900 and contains a mosaic of forests of different age, size, and composition. Hunters shot grouse over the entire area and provided data for our regional index. We made what we believe to be almost total counts of Spruce Grouse on study plots of ≥ 1 km^2, and James and Peck (1994) made transect estimates of densities of breeding birds including Ruffed and Spruce Grouse both in our study plots and in forests similar to them. Estimates of hare abundance were made from pellet counts along a line of ≥ 500 m in each study plot. Local estimates of abundance were made in young pine, medium aged pine, old pine, and old mixed conifer/deciduous forest, hereafter also called mixed forest (Figs. 1 and 2).

Table 1. Canopy height, cover of the ground (%) by vegetation, and species of plants making ≥ 10 percent of cover in local forests.

Forest	Young pine	Medium aged pine	Old pine	Old conifer/ deciduous
Age when described (years)	9-11	19-24	41-46	49-54
Mean distance from ground to canopy (m)[a]	0.5 jack pine	5 jack pine	13 jack pine	14 trembling aspen
Mean cover (%)[b]				
Trees				
Conifer	30 jack pine	70 jack pine	70 jack pine	20 black spruce balsam fir
Deciduous	30 trembling aspen			60 trembling aspen
Tall shrubs	20 pin cherry	20 green alder	30 green alder	50 beaked hazel mountain maple alder
Low shrubs	30 bush honeysuckle	50 blueberry sheep laurel sweet fern	40 sheep laurel blueberry	20 bush honeysuckle blueberry
Mosses	30	30	40	20
Herbs	30 aster bunchberry graminoids	20 trailing arbutus	20 bunchberry Canada may flower clintonia	20 clintonia wild sarsaparilla aster

a) Size of sample: young pine 128, medium aged and old pine 100, aspen 64, b) trees and tall shrubs, young pine 11, other forests 20; low shrubs, mosses, and herbs all forests 50.

Methods

Habitats were described by estimating the percentage coverage of the ground by vegetation at points along lines 500 m to 2.1 km in length in August. Data were obtained every 25 to 200 m within 1 m of a point for herbaceous vegetation (≤ 0.3 m in height), or 5 m for low shrub (0.3-1 m), tall shrub (1-3m), and trees (>3 m). Young jack pines were measured at points by a quadrat of 4 m^2 for low shrubs and higher layers, and 5 x 1 m^2 quadrats for herbs, graminoids, and mosses and lichens. The quadrats were those used for counts of hare droppings. Records in all habitats included height to lowest branches of the trees, species of most plants, and abundance of berries of blueberry *Vaccinium* spp. and bunchberry *Cornus canadensis*. Berries were counted in the quadrats and estimated in abundance in categories from 0 to 5 in an area approximately 5 m in radius from each point along the lines.

Regional indices of numbers of grouse were achieved by a road check of hunters on highway 560 (Fig. 1). The check was done in the opening week-end of each season, and from each hunter we obtained the number of days hunted, where, and the number of each species of grouse shot. A hunting day was six hours. Usually, we examined the birds taken. Local counts of Spruce Grouse were made in spring and summer using trained pointing dogs to locate virtually all males and females. From 1981-89, grouse were banded. In 1993, while some were banded, individual identification of most was from at least three sightings on a territory. Intensive search with dogs is thought to give an accurate count of breeding grouse (Bendell et al. 1972, Szuba 1982, 1989). Hares were indexed each August by counting and discarding their pellets in permanent quadrats of 1 m^2. Quadrats were placed five at a point, 3 m apart with one at each corner of the one in the centre (Fig. 1). Points of quadrats were located 100-200 m apart along lines of 500-1800 m through the centre of a study plot or forest. In 1982, pellets were counted on quadrats arranged in a different manner so we put cautionary brackets on the data obtained. Krebs et al. (1987) and MacLulich (1937) concluded that pellet counts gave accurate estimates of the absolute abundance of hares. We believe they give relative abundance at least. Hares and grouse were also counted from sightings and from their tracks in snow in forests and along roads through the regional and local study areas (Fig. 1).

Possible correlations between variables were tested with the Pearson product-moment correlation coefficient (r_{jk}) or the regression coefficient (b) (Sokal and Rohlf 1981). Means were tested by t-test and frequencies by X^2. Significance was at the $p \leq .05$ level.

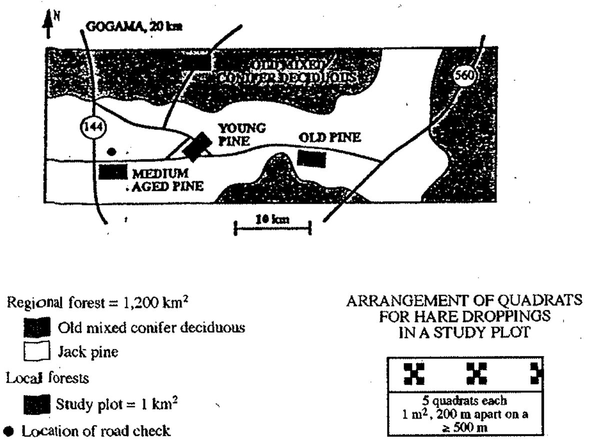


Fig. 1. Regional and local forests studied for populations of grouse and hares.

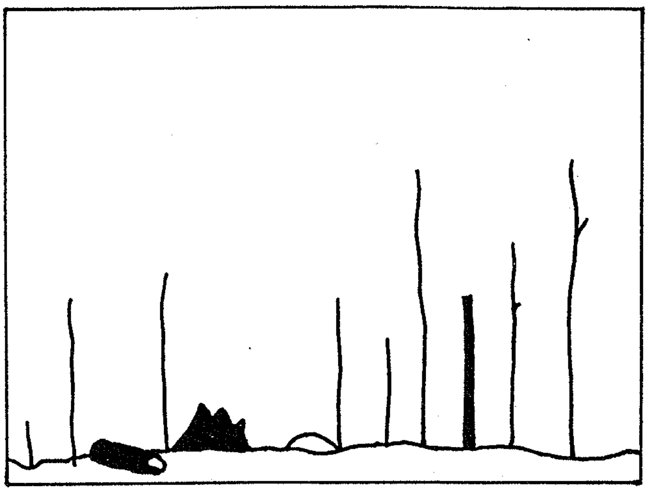


Fig. 2(a). Young pine, burned 1981, profile 1981.

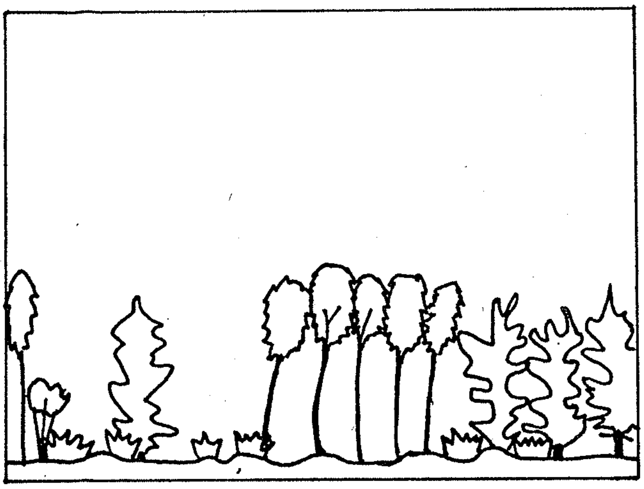


Fig. 2(b). Young pine, profile 1994.

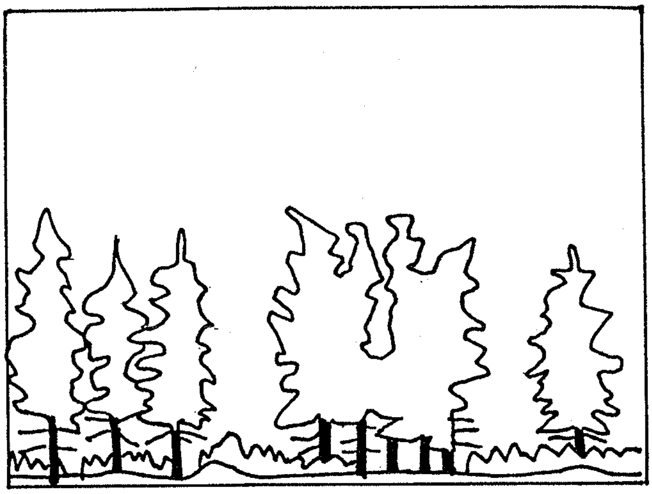


Fig. 2(c). Medium aged pine, seeded 1970, profile 1994.

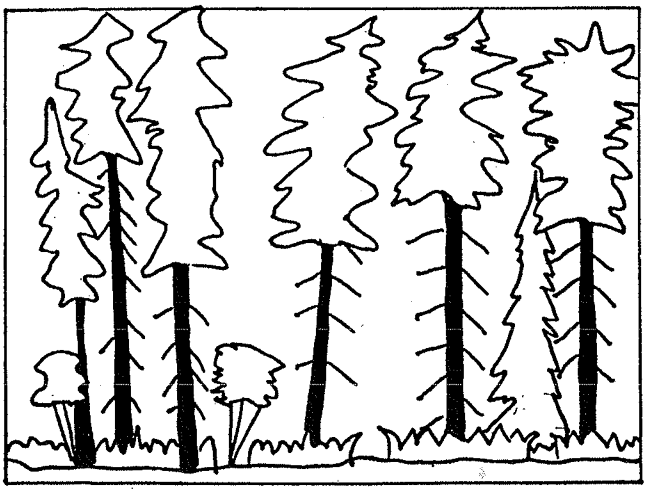


Fig. 2(d). Old pine, seeded 1948, profile 1994.

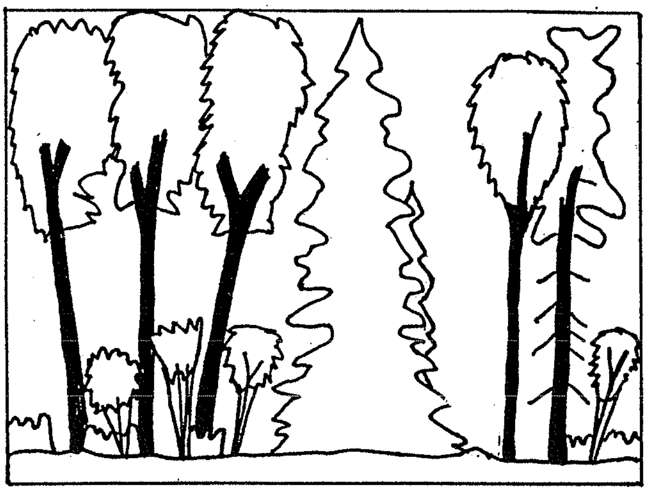


Fig. 2(e). Old mixed conifer/deciduous, logged 1940, profile 1994.

Figs. 2(a) - 2(e). Forests typical of regional and local areas.

Results

Amount of cover

The data (Table 1, Fig. 2 a-e) provide an estimate of maximum amount of cover. From October to June, most deciduous plants were leafless and the cover they gave was reduced. From December to March, there was 1 m or more of snow on the ground so that almost all low shrubs and shorter plants disappeared. Medium aged and old pine were alike in coverage, with a canopy of conifers, tall and low shrubs, herbs and mossses. However, in medium aged pine the canopy was much closer to the ground. Young pine was like old mixed forest in low shrub and moss cover. Both also had a large component of deciduous trees. But the tree canopy of young pine began almost at the ground and there was less coverage by tall shrubs and more coverage by herbs than in the mixed forest. In the mixed forest, the canopy began on average approximately 14 m above the ground, and for the conifers the distance ranged from 0 to approximately 12 m. Clearly, the forests were different in the amount and height of cover offered by the vegetation and this was most apparent in winter.

The young pine was similar to the medium aged pine until May 1981 when a fire of 380 ha reduced it to black ash and standing sticks of trees (Fig. 2a). By 1983, the area was scarified and planted to jack pine at a density of 5425 trees/ha. Like the mixed forest but unlike the other pine forests, the ground there was gently rolling. The young pine also differed in having a forest floor roughened by site preparation and a relatively large amount of fallen trees. In 1994 (Fig. 2b), the plot was a patchwork of dense stands of coniferous or deciduous trees with open areas of low shrubs and herbs. The young pine represented events in a new and rapidly growing forest of jack pine after fire.

Species of plants

Most of the cover was provided by a relatively few species of plants (Table 1). In the medium aged and old pine, jack pine was virtually the only tree. Jack pine is eaten all year by Spruce Grouse and provides most of the winter diet (Boag and Schroeder 1992, Robinson 1980). However, black spruce *Picea mariana* was invading all stands and made small patches of trees in the old pine. Trembling aspen *Populus tremuloides* equalled or exceeded the amount of tree cover provided by conifers in the young pine and mixed forest. It is a staple winter food of Ruffed Grouse (Gullion 1984). In the mixed forest, black spruce provided the most conifer cover followed by balsam fir *Abies balsamea*, jack pine and white spruce *Picea glauca*. Clearly, the mixed forest offered the greatest mixture of tree species. Tall shrubs were pin cherry *Prunus pennsylvanica*, green alder *Alnus crispa*, beaked hazel *Corylus cornuta*, and mountain maple *Acer spicatum*. Pin cherry, mountain maple and hazel are foods of Ruffed Grouse and snowshoe hares (Bump et al. 1947, Dodds 1987).

Among the low shrubs, sheep laurel *Kalmia angustifolia* is evergreen while the rest are deciduous. There were roughly equal amounts of the main shrubs in each forest. Sheep laurel and sweet fern *Comptonia peregrina* were not used as food by grouse or hares but the other two low shrubs, bush honeysuckle *Diervilla lonicera* and especially blueberry provided plant foods for hares and grouse and invertebrates for chicks (De Franceschi and Boag 1991, Robinson 1980).

There were many herbs in the forests but only a few covered much of the ground. Trailing arbutus *Epigaea repens* flowers were preferred food of breeding female Spruce Grouse (Naylor and Bendell 1989). Bunchberry yielded fruits eaten by hares and grouse. While graminoids are eaten by grouse and hares, aster *Aster macrophyllum* and *Clintonia borealis* apparently are not (Bump et al. 1947, De Franceschi and Boag 1991, MacLulich 1937, Naylor 1989). The use of wild sarsaparilla *Aralia nudicaulis* as food by hares and grouse is unknown. Herbs that made relatively little cover but were frequently present included creeping snowberry *Gaultheria hispidula* and gold thread *Coptis trifolia* in old pine, and star flower *Trientalis borealis* and Canada mayflower *Maianthemum canadense* in mixed forest, and less frequently others.

As with cover, the forests differed in the abundance of species of plants making up most of the cover. The pines were virtual monocultures of jack pine, with low shrubs of blueberry and sheep laurel. Medium aged pine was distinctive in the large amount of trailing arbutus. Old pine contained the most moss and bunchberry. The mixed forest had the greatest diversity and amount of tree and tall shrub species, some of which were scarce in other forests. However, it contained relatively little blueberry. The relative diversity of the mixed forest may be explained by variations in site and the natural regrowth of forest after logging and fire. Clearly, the study forests were different in cover and relative abundance of plant species. However, all forests were simple in that few plant species contributed much to cover.

Abundance of berries

In August, from 1988 to 1993, the abundance of blueberries and bunchberries was assessed in each forest. The berries, especially blueberry, were heavily eaten by grouse and hares. The ratings were pooled by forest to yield total number of estimates, the frequency of each category of estimate, and the average estimate for the number of years done. The number of estimates for each forest ranged from 55 to 82. The old pine clearly contained more blueberries (X^2, $P < 0.001$) and bunchberries (X^2, $P < 0.001$) than the other forests. In order of greatest to least average category for blueberries the forests were: old pine 0.7, young pine 0.3, medium aged pine 0.2, and mixed forest 0.1. For bunchberries, the ranking was: old pine 0.8, mixed forest 0.2, young pine 0.1 and medium aged pine 0. The category for abundant berries was 5.0. Thus no forest contained large amounts of berries, most were found in old pine, and the other forests were similar in the relatively low abundance of these fruits. Results from counting berries in quadrats were consistent with the data presented. Berry production was greatest in old pine and least in medium-aged pine.

Estimates of the regional abundance of grouse

The regional index of grouse by road check of hunters raises questions about what the data represent. We assume that the data reflect the fall abundance of grouse and are useful as relative measures. Numerous studies show that hunting success indicates numbers of Ruffed Grouse (e.g. Kubisiak 1984). Szuba (1982) showed that the number of Spruce Grouse observed per hour in medium aged pine correlated well with breeding density.

The road check data were gathered during the opening two days of the season which would reduce the effect of depletion of population by hunting. Moreover, there was a strong positive and direct correlation between number of days hunted or hunting effort and number of grouse shot (for Ruffed Grouse b=0.87, p=0.0001, and for Spruce Grouse b=0.70, p=0.001). The deviations from the regression lines, while variable, showed no trend for either species and were not or only weakly correlated between numbers of each species shot per hunter per day (Ruffed (r_{jk}=0.16, p=0.63), Spruce Grouse (r_{jk}=0.64, p=0.03)). Thus, hunter success presumably reflected numbers of grouse in the field and was sensitive to annual differences in abundance.

The regional indices of fall abundance of grouse from road checks of hunters show no statistically significant trend in the abundance of Ruffed Grouse (r_{jk}=0.47, p=0.12) (Fig. 3). However, there was an increasing trend in the regional numbers of Spruce Grouse (r_{jk}=0.73, p=0.0062).

The average number of hunters checked each year from 1981 through 1992 was 115 with a range of 52-175. Each hunter shot on average 0.54±S.E.0.04 Ruffed and 0.40 ±S.E.0.03 Spruce Grouse per day. The difference is statistically significant (t-test) suggesting that Ruffed Grouse were selected by hunters, more available, more abundant, or some combination of all three factors.

The annual numbers of Ruffed Grouse shot apparently fluctuated more (C.V. 32%) than those of Spruce Grouse (C.V. 28%) which showed relatively litle change from year to year. While the data span but 12 years there is little evidence of the classic 10-year cycle of abundance in either species, especially in the case of the Spruce Grouse. We compared birds per hunter per day for each species in the same and adjacent years and how numbers of Spruce Grouse in one year compared with numbers of Ruffed Grouse the year before and the year after. No correlation was significant which suggests that the regional populations of Spruce and Ruffed Grouse were independent.

Numbers of hunters

We compared the number of hunters checked each year with hunter success the previous year. The correlations were positive and statistically significant for each species and together suggesting that hunter success in one year influenced the number of hunters hunting in the next. The correlations were for Ruffed Grouse, r_{jk}=0.76, p ≤0.005, for Spruce Grouse, r_{jk}=0.52, p ≤0.05, and together r_{jk}=0.55, p ≤0.01. The stronger correlation with Ruffed Grouse suggests that this species attracted more hunters.

Estimates of numbers of snowshoe hares

The local index of hare numbers showed fluctuations in abundance that varied within and between forests (Fig. 4). None of the data within forests suggest a 10-year cycle in population. However, there were striking differences and similarities in abundance and changes in abundance.

There were apparently similar numbers of hares in young pine prior to the fire of 1981 and in medium aged pine and mixed forest from 1986 on. Remarkably, hares in medium aged pine and mixed forest, from 1986 on, apparently had the same annual average abundance (t-test) and simultaneous fluctuations in abundance (r_{jk}=0.87, p=0.005). There were few hares in old pine compared to the other forests (t-test). However, there was an apparent increasing trend in numbers in old pine from 1986 on (r_{jk}=0.80, p=0.02). The pellet counts suggest that hares were most abundant when young and medium aged pine were approximately 12 years of age. Hares were apparently at low density when pine, as in old pine, became 34 years of age.

The wildfire of May 1981 in medium aged pine forest gave an excellent opportunity to measure the impact of habitat change on hares and grouse. Prior to the fire, all three species were present (Spires and Bendell 1983). Immediately after the fire, from search with dogs, and the absence of sightings along roads (Spires and Bendell 1983) and later from searches for grouse and tracks in snow, grouse and hares disappeared. From our regular quadrat counts, hares did not appear in the young pine until 1988, an apparent absence of seven years. Thereafter, there was an obvious increase in the abundance of hares which apparently continues (Fig. 4). Counts of tracks in snow along the quadrat line in March 1993 were high, reflecting the abundance of hares and suggesting there were resident animals. Hares were present in adjacent and nearby medium aged pine and mixed forest from at least 1981 on, suggesting that habitat and not lack of colonists explained the new population. There has been an obvious change in the vegetation of the young jack pine from an open landscape, particularly in winter (Fig. 2a), through a scattered herb and shrub stage, to the present mixture of herbs, shrubs, and trees (Table 1, Fig. 2b).

Estimates of the local abundance of grouse

We have not found Spruce Grouse in young pine forest, and Ruffed Grouse or their tracks and droppings were seen there only four times. James and Peck (1944) also recorded no Spruce Grouse in this habitat but did tally 5.0/km^2 drumming male Ruffed Grouse in 1988. In other years in 1987 - 1992, neither species of grouse was recorded. They also studied a jack pine plantation of seven years of age in 1985, comparable to our young pine of the same age. Neither Ruffed nor Spruce Grouse was found. Both species of grouse occurred in nearby forests throughout the studies. Hence, habitat was apparently still inadequate for grouse in the young pine. Hares, however, had moved into, become abundant, and were increasing there.

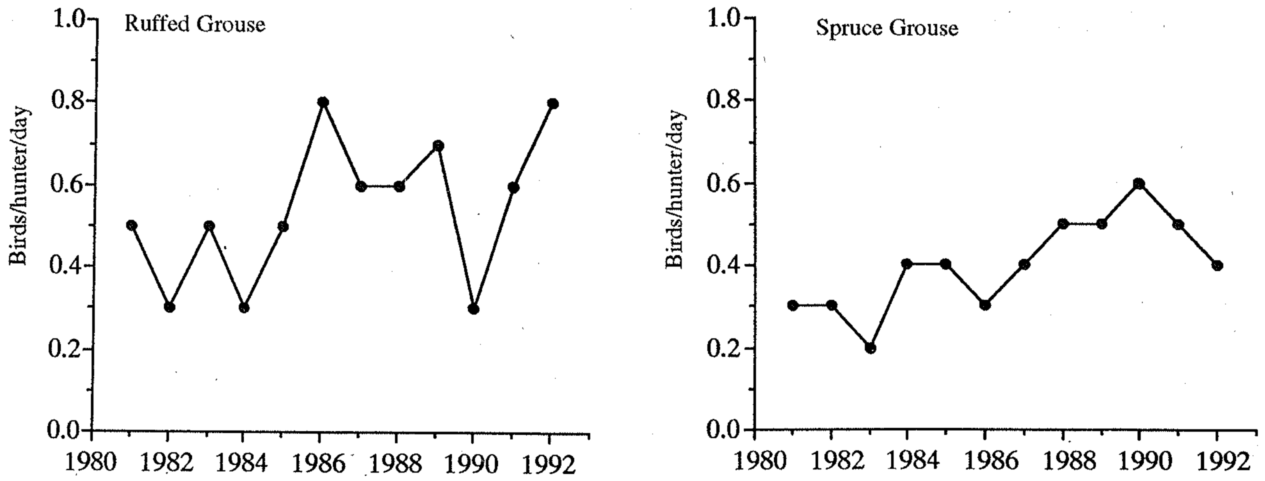
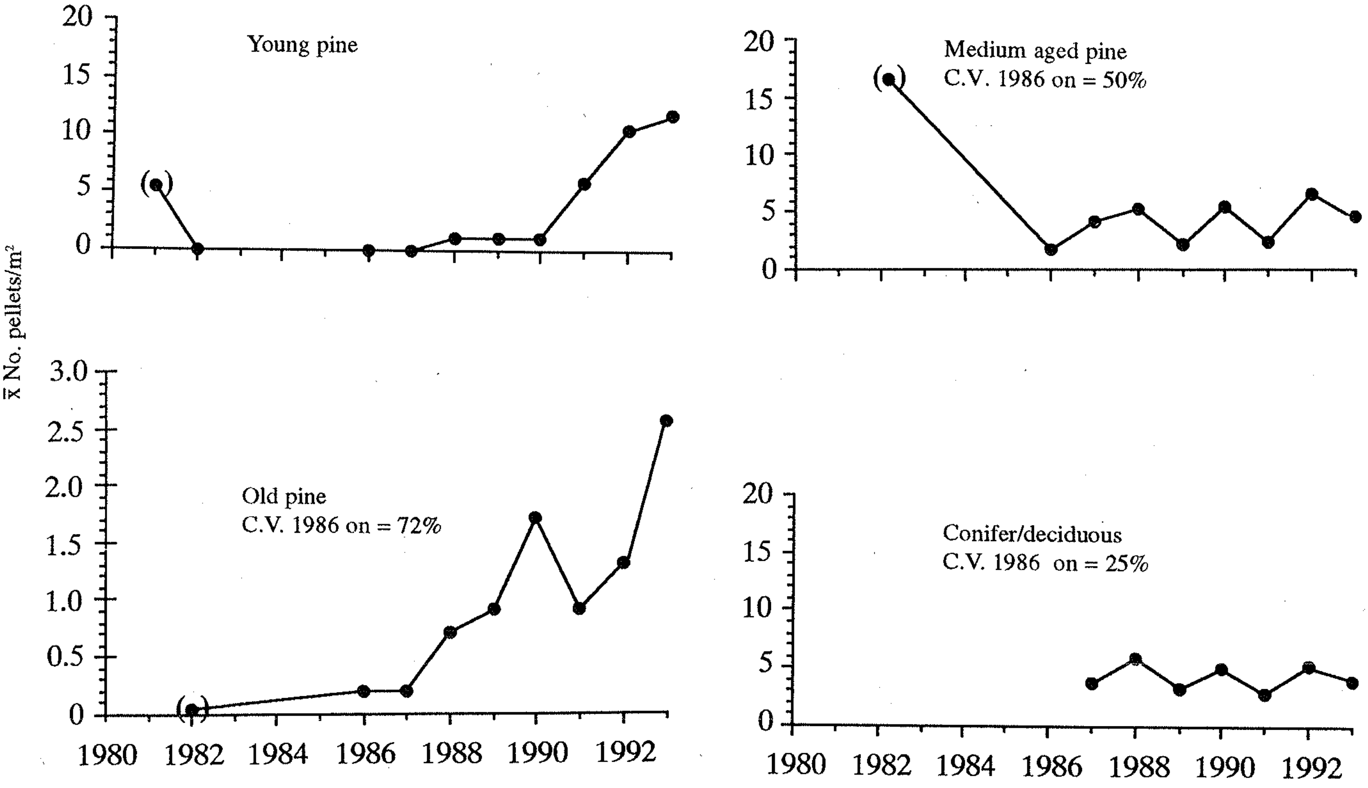


Fig. 3. Regional indices of grouse by road checks of hunters on the opening two days.



n Quadrats each forest each year, 1982, 25; other years 30-50.

Fig. 4. Index of abundance of hares in local forests from pellet counts.

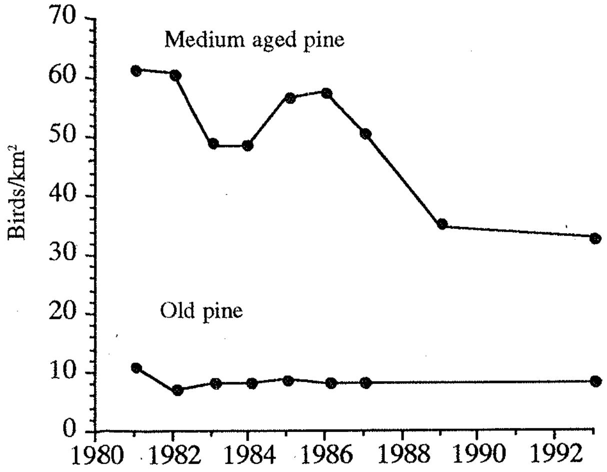


Fig. 5. Breeding density of Spruce Grouse in local forests determined by search and banding.

Spruce Grouse were exceptionally abundant in medium aged pine at 11-17 years of age (Fig. 5), and close to the highest recorded densities for the species (Szuba and Bendell 1983). However, from 1981 to 1993, there was a significant decline in the numbers counted, with relatively little variation about mean density (r_{jk}=-0.84, p=0.004, C.V. 21%). In the old pine, Spruce Grouse remained at a relatively low and remarkably stable density (C.V. 14%) over the same period.

Ruffed Grouse were occasionally seen by us in the medium aged and old pine but none was established as a breeding bird. Ruffed Grouse were in adjacent mixed forests throughout the study. James and Peck (1994) estimated the density of breeding birds in medium aged and old pine from 1985 to 1992. They did not find Ruffed Grouse. They also studied a young mixed forest 17 years of age in 1985, and an old mixed forest comparable to our old mixed forest. The young woods from 1985 through 1988 contained an estimated average density per year of Ruffed Grouse of 26 birds/km^2 with a range of 10-44. The old mixed woods from 1986 to 1988 had an estimated average density of 18 birds/km^2 with a range of 16-20.

Relationships between hares and grouse

Like Spruce Grouse, hares were abundant in medium aged pine with few in old pine. However, there was no correlation between numbers of hares and Spruce Grouse in the same and adjacent years in either forest. In medium aged pine, Spruce Grouse apparently were in decline while hares declined and then became more or less stable in abundance (Figs. 4, 5). In old pine, Spruce Grouse remained stable in abundance while hares apparently increased (Figs. 4, 5). On a regional scale, there were no correlations between regional indices of Spruce and Ruffed Grouse and hares in the same and adjacent years in the medium aged pine and mixed forest. Hence, the local and regional populations of grouse and hares considered here were apparently independent.

Discussion

Our objectives were to obtain counts of populations in different but nearby habitats, compare habitats and species, and attempt to explain apparent differences in abundance. We are aware of some of the biases that may compromise the accuracy of our methods. However, we have tried to check our indices of populations and believe them to be accurate to the extent used here. Our other measures of abundance such as counts of tracks in snow and sightings along roads support the results we have obtained. An obvious shortcoming in revealing trends in populations is the number of years of observation. However, we believe that if there had been large changes in the abundance of grouse and hares our indices should have revealed them. This was certainly the case in young jack pine where hares went from none to abundance in five years.

Cycles or fluctuations

The data suggest that numbers of Ruffed Grouse and snowshoe hares fluctuated annually without showing a 10-year cycle. Spruce Grouse were relatively stable in abundance and in old jack pine remarkably so. While not all populations of grouse and hares are cyclic (Keith 1963, Smith 1983, Theberge and Gauthier 1982), those in northern locations are reputably so. Sinclair et al. (1993) claim that hare populations cycle synchronously throughout the entire boreal forest and as an indirect result of sunspots. Clarke (1936) considered Ruffed Grouse and MacLulich (1937) hares to be cyclic throughout their range in Ontario including forests south of our study area. A general explanation for the phenomenon is that northern habitats are simple in ecological complexity and therefore populations in them are prone to fluctuation (Elton 1958, Odum 1971, and others). Our study forests qualify as northern, and the plantations of jack pine were simple habitats consisting of few species of plants and three main layers of vegetation. We conclude that not all populations of Spruce and Ruffed Grouse and snowshoe hare are cyclic and that northern location and simplicity of habitat may not generate cyclic fluctuation.

Expanse of habitat is also offered as a factor causing cycles, so that the more patchy the forest landscape the less the tendency for populations to cycle (Moss et al. 1982). This may be relevant to our results and needs further study. We note, however, that mixed forest covered a large part of our study area and far beyond, yet our sampling failed to detect cycles in Ruffed Grouse and hares.

The interpretation of amount of annual fluctuation of populations of grouse and hares is confused by different methods and season of indexing. With grouse, fall numbers generally fluctuate more than those in spring, and regional estimates were made in fall while local estimates were made in spring. The estimates of hare abundance represent an annual density. The largest coefficients of variation of population fluctuations were those of Ruffed Grouse and snowshoe hare. From the data of James and Peck (1994), the C.V. for a spring population of Ruffed Grouse in one forest measured over four years was 66%. This suggests that both spring and fall populations showed relatively large fluctuations. Compared to Ruffed Grouse and hares, the fall and spring populations of Spruce Grouse were relatively constant and remarkably so in old pine. In the simplest of habitats, the old pine, Spruce Grouse apparently fluctuated the least (C.V. 14%) and hares the most (C.V. 72%). Hares apparently fluctuated least (C.V. 25%) in the relatively complex habitat of the mixed forest. Hence, the simple habitat may have increased the fluctuations of hares but not of Spruce Grouse. Ruffed Grouse in spring and fall fluctuated much more than hares in mixed forest. Since there were no correlations between the fluctuations of grouse and hares, the causes of fluctuations probably included the population response of each species to its specific habitat requirements. Ruffed Grouse and hares have a higher birth rate than Spruce Grouse and both are most abundant in the early stages of forest succession. Thus, both reproduction and habitat may be potentially more variable for Ruffed Grouse and hares than for Spruce Grouse and hence the smaller variation in abundance of Spruce Grouse.

Trends and densities of grouse and hares

Spruce Grouse populations were apparently increasing regionally but declining or stable locally. Ruffed Grouse showed no trend either regionally, or locally from the counts by James and Peck (1994). The study region was a patchwork of logged and replanted pine forests and perhaps an increasing proportion of medium aged pine resulted in increasing numbers of Spruce Grouse. By the same argument, mixed forest was relatively unchanged so that Ruffed Grouse showed no trend in abundance. From 1986 on, hares were increasing in abundance in the young pine and, surprisingly, also in the old pine. Within medium aged pine and mixed forest they showed no apparent trend in populations. As with the grouse, change in vegetation affecting hares is the most likely explanation for the change in hare abundance.

The road check index of populations suggested that there were more Ruffed Grouse than Spruce Grouse in the study region. Hunters did apparently shoot more Ruffed Grouse. This may be explained by the greater amount of habitat for Ruffed Grouse in the regional area and the potentially larger production of chicks in the fall. However, Ruffed Grouse were more vulnerable to hunters because they frequented roads and fed in leafless trees. Spruce Grouse remained within the coniferous forest. Moreover, our results indicate that hunters may select for Ruffed Grouse. This suggests that the hunter index of abundance was biased in favour of Ruffed Grouse and should not, at present, be used to compare the actual numbers of the two species. Nevertheless, if the increasing trend of Spruce Grouse in the harvest continues, numbers killed will presumably exceed those of Ruffed Grouse.

The numbers of hunters fluctuated from year to year and we obtained a strong regression between hunting success in one year and the number of hunters hunting in the next. An obvious explanation is that when hunters were successful they returned and told others, resulting in an increased participation in the hunting for grouse.

The wide variations in abundance of the three species in different habitats separated by short distances shows the need for considering the extent of a particular habitat in extrapolating densities. For example, the average numbers of pellets/m^2 in young, medium aged, and old pine in 1992 were 11.0, 7.0, and 1.3, respectively, a 7-10 fold difference over distances between habitats of less than 20 km. After the fire in 1981, hares were not detected in the young pine until 1988. Similarly, in 1981, Spruce Grouse were six times as numerous in medium aged compared to old pine. Both Spruce Grouse and apparently hares were most abundant in 11-12 year old pine and declined as the forest aged. Parker (1984) recorded the same phenomenon in hares in plantations of spruce. From our work and that of James and Peck (1994), maximum densities of Spruce and Ruffed Grouse/km^2 in spring were, respectively, in young pine 0, 10; medium aged pine 62, 0; old pine 11, 0; medium aged mixed wood 0,44; and old mixed wood 0, 20. Clearly, Spruce Grouse were in pine forest, Ruffed Grouse in mixed forest, and hares were in both. Robinson (1980) found similar habitat preferences by Ruffed and Spruce Grouse in Michigan. We show that densities of both varied over a short distance associated with the kind and age of forest. Thus, regional densities of grouse and hares would reflect the amount of local areas in different forests.

The decline in local density of Spruce Grouse with increasing age of forest agrees with the findings of Szuba and Bendell (1983) and Boag (1991). However, the population in old pine has remained stable while the forest aged. The densities of Ruffed Grouse conform with the view of Gullion (1984) that this species does best in early successional stages of aspen forest. He reported maximum densities in spring of 49 or more grouse/km^2. Note that the maximum density estimated for Ruffed Grouse in medium aged mixed forest in our region approached that given by Gullion (44 vs. 49/km^2). Our mixed forests contained large amounts of conifers which contradicts the notion that purely deciduous forests, especially of young aspen, produce the highest densities of Ruffed Grouse.

We have already recorded elsewhere the highest spring density of Spruce Grouse reported. This was 80/km^2 in medium aged pine near our study area (Szuba and Bendell 1983). In the medium aged pine of this study, the highest density was apparently 62/km^2. Thus, maximum spring densities of Spruce Grouse on our study area exceeded those of Ruffed Grouse, and over its entire range as surveyed by Gullion (1990).

Estimates of actual densities of hares from counts of droppings are subject to many sources of bias. However, Krebs et al. (1987) state that "fecal pellet counts provide a quick and accurate method for snowshoe hare censuses on an extensive scale." They provide a simple function for converting average numbers of dropping/quadrat 0.155 m^2 into hares/ha. Similarily, MacLulich (1937) converted pellets/m^2 into hares/ha. By the method of Krebs et al., our maximum densities were in medium aged pine in 1982 at 0.77 hares/ha, and in young pine in 1993 at 0.62 hares/ha. By the method of MacLulich, the values were 7.0 and 4.9 hares/ha. Krebs et al. show maximum densities of hares at

12/ha. The data of MacLulich suggest a maximum density of 12.7 hares/ha in forests in Ontario more like ours than those of Krebs et al. who sampled in the Yukon. In a forest comparable to our mixed forest, from the data of MacLulich, densities were 3.5 hares/ha compared to ours of 1.5 to 3.0 hares/ha. We believe that the estimates of hare density by MacLulich's calibration are the closer to the truth. If so, hare densities in jack pine in our study area were apparently less but comparable to those in a range of forest types in Ontario and the Yukon.

Habitat requirements and population control

What factors caused the densities and changes in densities of grouse and hares which we observed? Because Spruce and Ruffed Grouse lived in different habitats it is unlikely that they competed for food. However, the hares lived in all habitats used by grouse so there might be associations among them. Before the fire that partly created the young pine, hares were abundant and Ruffed and Spruce Grouse were present. Immediately after the fire, all three disappeared from the area of the burn although each was present in adjacent forests. Within a few days, there began a lush growth of vegetation on the burn, and in 1983 it was planted to jack pine. Most of the new plants were foods of grouse and hares. Yet hares increased in this young pine forest only after 10 years of regrowth, breeding Ruffed Grouse were recorded at a low density seven years after the fire and not in three later years, and they and Spruce Grouse were apparently absent to the present time. This sequence of events suggests that cover initially limited the numbers of hares and grouse and that the grouse required more cover than the hares. Hares increased in abundance in the young pine when conifer tree cover became approximately 30%. Hares and Spruce Grouse were also apparently most abundant in the medium aged pine when it was 9 and 10 years of age, respectively.

The sporadic occurrence of Ruffed Grouse in and the absence of Spruce Grouse from the young jack pine forest to the present time suggests that both grouse require more tree cover than the hares. The appearance of the Ruffed Grouse is in keeping with its use of thickets of aspen and other tall deciduous shrubs. Why it disappeared again is unknown. Nevertheless, its occurrence suggests it required less tree cover than the Spruce Grouse. The high abundance of Spruce Grouse in the medium aged pine when it was nine years of age suggests that the young plantation now at 11 years of age should have a population of this grouse. However, high densities of Spruce Grouse occurred in young plantations of jack pine, including the medium aged forest, when cover by pine was approximately 60% (Szuba and Bendell 1983). Hence, the young jack pine with 30% coverage by pine may have provided inadequate conifer tree cover for Spruce Grouse.

As tree cover ages, populations of Spruce Grouse and Ruffed Grouse decline. In this study, lowest populations of grouse and hares occurred in old forest and the dense population of Spruce Grouse in medium aged forest declined. This cannot be explained by tree cover alone because all old forests had at least 60% cover by trees. The increasing population of hares in the old pine is an apparent contradiction to the rule of fewer numbers in old forest. However, black spruce was invading the old jack pine and provided cover closer to the ground. This is where hares and Spruce Grouse were found and may explain the change in number of hares.

Cover obviously affected the abundance and distribution of grouse and hares because none occurred where cover was inadequate. Once populations were established we ask how density and changes in density were caused. Cover might affect rates of predation and/or the supply of food and so drive populations. Recent work on Spruce Grouse in our study area indicates that mortality from predation cannot account for differences between populations in medium aged and old jack pine (Bendell and Szuba 1994, Szuba 1989). Naylor (1989) and Naylor and Bendell (1989) show that foods required by hens for reproduction may limit density, and dense populations were associated with the abundance of trailing arbutus, a major food of breeding hens. Foods for reproduction may also include the insect food required by very young chicks (Lattner 1982) who found that insect foods were more abundant in medium aged as compared to old pine forest. And we have many more data from all forests on the abundance of invertebrates used as food that support this conclusion.

The apparent independence of numbers of grouse and hares suggests that predation and interspecific competetion were not factors affecting established populations. Remarkably, hares were apparently at the same average density and fluctuated together in medium aged jack pine and old mixed forest. These were forests of quite different cover or structure which should affect predation and cause differences between populations. The striking similarity between populations again suggests that predation was not causing them. Note that a high density of hares occurred with a high density of Spruce Grouse in medium aged pine and without this grouse in young pine. This reinforces the conclusion that the populations of each may be independent.

Examining the forests for foods, blueberry and trailing arbutus were most abundant in the medium aged pine and least in the young and old pine which correlates directly with the abundance of Spruce Grouse. On the other hand, fruits of blueberry and bunchberry were most abundant in old pine where relatively few Spruce Grouse and hares were found, and few where grouse and hares were abundant. This suggests that the berries were not critical foods and perhaps most were eaten where grouse and hares were abundant. We conclude that given cover, the abundances of grouse and hares in our area were caused by the food supply which differs for each. As pine and mixed forest ages, critical foods for grouse and hares decline and population decline follows. And the greater fluctuation in population noted for hares and Ruffed Grouse may be partly explained by a more variable food supply to each.

Plantations of pine and wildlife

Forests of jack pine and plantations generally are considered to be poor habitats for wildlife (Erskine 1977, Racey et al. 1989, Elton 1958, and others). What is meant by poor requires definition and should include biodiversity, abundance, persistence, value, and other qualities. James and Peck (1994) concluded that the pure jack pine forests of our study area provided population densities of birds comparable to those normally found in boreal spruce forests. Where jack pine were mixed with deciduous trees, and at about 20 years of age, numbers of species and densities were increased. Older mixed and pure pines were similar in species abundance and richness. Here, we report for a medium aged pine plantation, exceptional densities of Spruce Grouse and densities of snowshoe hares comparable to a range of forest types in Ontario. Moreover, these abundances have lasted 11 to 12 years at least. Medium aged jack pine was as productive of hares as old mixed forest. And medium aged mixed forest where jack pine was the dominant conifer apparently produced spring densities of Ruffed Grouse comparable to high density elsewhere in the range of the species. The abundance of hares and grouse may affect the occurrence of other wildlife such as marten *Martes americana* (Thompson and Colgan 1994) and lynx *Lynx canadensis* (Wagner 1979). Clearly, to the extent discussed, plantations of jack pine may be productive of wildlife, and this probably depends upon the presence of a rich shrub and herb layer used primarily as food.

Acknowledgements - Our thanks to the many who have provided data, assistance, and advice. We particularly appreciate the foundation of this work by B.J. Naylor and K.J. Szuba. K.J. Szuba counted local populations of Spruce Grouse from 1981 to 1987. Numerous graduate students and summer assistants helped with the counting of grouse, hare droppings, and the road check of hunters. J.J. and L. Bendell kindly typed numerous versions of the manuscript, some in response to the excellent suggestions of D. Jenkins and T. Willebrand. Financial support was from the Ontario Ministry of Natural Resources (OMNR) and the National Science and Engineering Research Council of Canada (NSERC). Personnel of OMNR Gogama and many hunters were most cooperative. E.B.Eddy co-provided temporary lodging.

Summary

Our objectives were to describe the annual numbers of Ruffed and Spruce Grouse and snowshoe hares and seek interrelationships among the numbers of each species and habitat. A long term purpose is to find how numbers are controlled. From 1981 to 1992, we obtained an index of the regional abundance of Ruffed and Spruce Grouse from the road check of hunters on the opening two days of the hunting season near Gogama, Ontario. Hunters shot grouse over an area of approximately 1,200 km^2 of jack pine and mixed conifer/deciduous forest. Spruce Grouse and hares were counted on study plots of 100 ha in pine forest. Spruce Grouse were counted in pine from 1979 through 1993 by search with dogs, banding, and mapping territories. An index of hare abundance was obtained from 1982 through 1993 by pellet counts in permanent quadrats in the pine study plots and along a line in conifer deciduous (mixed) forest. The local plots and line represented regional forests and included three plantations of pine, 0-10, 11-23, and 33-45 years of age, and a mixed forest 41-53 years of age. Ruffed Grouse were in mixed forest, Spruce Grouse were in pine, and hares were in both.

From 1981 to 1992, 52 to 175 hunters on the opening two days of each year shot per hunter per day an average 0.54 ± S.E. 0.04 Ruffed and 0.40 ± S.E. 0.03 Spruce Grouse. From 1979 to 1993. numbers of Spruce Grouse ranged from none in young pine to approximately 60 per km^2 in medium aged pine. Hare numbers varied from none in early young pine to an average of approximately 17 pellets per m^2 (possibly 7.0 hares/ha) in young/medium aged pine.

Preliminary analyses suggest that there were irregular fluctuations but not cycles in populations of hares, Spruce and Ruffed Grouse, with less variation in populations of Spruce Grouse. There was no correlation between numbers of Ruffed and Spruce Grouse and hares in the same and adjacent years. The populations of the three species were apparently independent. Hares and Spruce Grouse were abundant in medium aged pine and few in old pine. Spruce Grouse increased regionally but declined in medium aged pine. Hares increased in young and old pine. Regional populations of Ruffed Grouse, and hares in medium aged pine and mixed forest, showed no trend. Hares were equally abundant in late young pine, medium aged pine, and mixed forest and fluctuated synchronously in the latter two habitats. The numbers of hares, Ruffed and Spruce Grouse were controlled by tree cover and most likely by the supply of the different kinds of food required by each.

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Populations of Capercaillie and Hazel Grouse in large natural and logged forests in northern Russia, 1950-92

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Introduction

Most Scandinavian grouse populations decreased dramatically in numbers during the latter part of the 20th Century (Joensen 1967, Marcström 1979, Hjeljord 1980, Järvinen and Väisänen 1984). The causes of these declines are not well understood but the pattern is similar in many European countries (Hudson and Rands 1988). Modern forestry, which may affect the birds both directly through habitat deterioration and indirectly by causing increased predation pressure, has been proposed as the main reason for the decline of Scandinavian forest grouse such as Capercaillie *Tetrao urogallus* and Hazel Grouse *Bonasa bonasia* (e.g. Marcström 1979, Lindén and Rajala 1981, Järvinen and Väisänen 1984, Rolstad and Wegge 1989, Swenson 1991, Wegge et al. 1992).

The dynamics of grouse populations in areas of large undisturbed forests are therefore of particular interest. Here, we give data from a 40-year study of Capercaillie and Hazel Grouse in the Pechora-Illych Nature Reserve in northern Russia, the largest area of pristine forests in Europe west of the Ural mountains (Fig. 1).

The study area had two parts: a smaller section surrounded by logged forest and a larger section located within wide stretches of undisturbed forest.

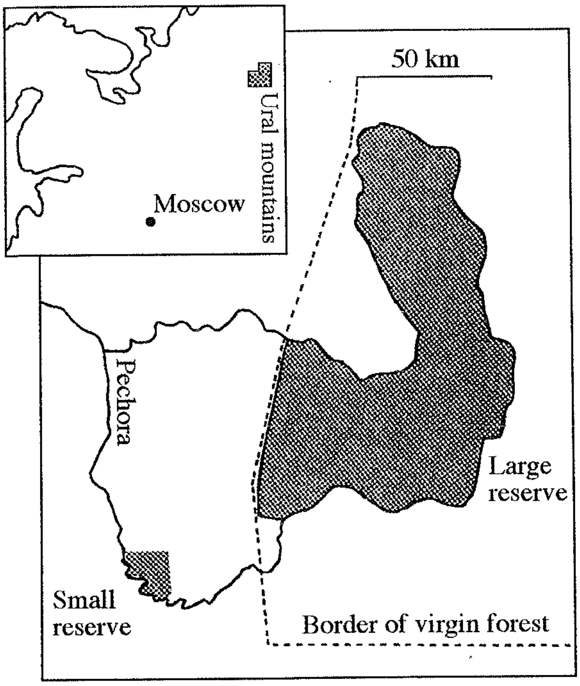

Fig. 1.Location of the small and large sections of the Pechora-Illych Nature Reserve, Ural mountains, Russia.

Dispersal and predation have been proposed as important links between population changes of grouse and industrial forestry (Wegge et al. 1992). Sub-adult Hazel Grouse and male Capercaillie have short dispersal distances while female Capercaillie may move longer distances (Koivisto 1963, Swenson 1991, Wegge et al. 1992). If dispersal out of the reserves is important for the maintenance of population numbers, we would expect this to have less effect on Hazel Grouse than on Capercaillie.

To test the assumption that modern forestry causes an increase in number of predators (Storaas and Wegge 1985, Henttonen 1989), we compared the abundance of red fox *Vulpes vulpes* and mustelids within the reserve and in the logged forests surrounding the reserve and also investigated changes in densities of these carnivores since the start of intensive logging in the upper Pechora region. We also compared population fluctuations of small rodents with numbers of stoats *Mustela erminea* and grouse and discuss grouse abundance and fluctuations in the upper Pechora region in relation to grouse populations in managed forest in Finland.

Study area

The Pechora-Illych nature reserve is located around the headwaters of the Pechora river, in the north-eastern corner of European Russia (62°N, 57°E). The forests of the reserve are under natural disturbance regimes, mainly fire. The main reserve of 705,500 ha lies within a continuous belt of virgin forest, extending for approximately 3 M ha along the western slopes of the Ural mountains. A smaller isolated reserve of 15,800 ha lies 75 km to the south-west of the main reserve (Beshkarev et al. 1995) (Fig. 1). Most of the forests surrounding this reserve have been logged by conventional clearcutting methods. In 1993, the small forest reserve together with adjacent uncut forest covered about 20,000 ha. Logging started in the 1950s, becoming more intensive after 1970. In 1993, c. 10% of this forest was aged under 10 years, 40% 10-50 years, 35% 50-100 years and 15% old growth. Clearcuts and forest blocks were usually smaller than 50 ha. Clumps of trees as well as single trees of little commercial value and all trees within 50 m of rivers and creeks have been left uncut.

Spruce *Picea abies* and birch *Betula* spp. dominate the forests of the main reserve, with a 9-10% intermixture of cembra pine *Pinus cembra* and fir *Abies sibirica*. The forest of the smaller reserve is typical of the flat taiga of northern Russia west of the Ural, with pine *Pinus silvestris* as a dominant species and spruce occurring in narrow corridors

Table 1. Age and species composition of forests along the transect routes of the small (pine-dominated) and large (spruce-dominated) sections of the Pechora-Illych Nature Reserve, North Ural, Russia, 1988. Figures give proportions (%) of transects within even-aged forest stands.

	Proportions (%) of forest in five age groups					
Species	0-20	21-40	41-80	81-160	161-300	Total
Small reserve:						
Picea abies	0.0	0.0	0.1	1.7	5.5	7.3
Abies sibirica	0.0	0.3	0.0	0.0	0.1	0.4
Pinus cembra	0.0	0.0	0.0	0.2	0.3	0.5
Pinus silvestris	0.0	9.4	14.1	23.2	36.6	83.3
Larix sibirica	0.0	0.2	0.0	0.0	0.0	0.2
Betula sp.	1.1	4.1	1.2	1.9	0.0	8.3
Total	1.1	14.0	15.4	27.0	42.5	100.0
Large reserve:						
Picea abies	0.2	0.4	1.8	26.4	14.8	43.6
Abies sibirica	0.1	0.0	0.2	4.8	1.3	6.4
Pinus cembra	0.0	0.0	0.0	1.8	2.4	4.2
Pinus silvestris	0.0	0.0	0.0	4.8	1.7	6.5
Larix sibirica	0.0	0.0	0.0	0.4	0.0	0.4
Betula sp.	2.1	4.6	20.1	9.7	0.0	36.5
Populus tremula	0.0	0.2	1.4	0.8	0.0	2.4
Total	2.4	5.2	23.5	48.7	20.2	100.0

along rivers and streams and with frequent mires. About 70% of the forest along the routes used for counts was more than 80 years old and had a typical old growth structure (Table 1). Hunting was permitted outside both reserve sections but the general public had no access to the reserve itself.

Methods

Estimates of numbers of Capercaillie and Hazel Grouse by route transects were conducted in both reserve sections during the last week of August and first week of September in each year from 1953-1992, providing an unbroken 40-year data set. A three-man team 20 m apart advanced on a front, thus covering a strip 60 m wide. The relative density indices were calculated from bird observations within this 60 m belt. The method was originally developed by Semenov-Tian-Shansky (1960), and a similar transect method has been carried out on a country-wide basis in Finland since 1962 (Rajala 1974). Within the large reserve, five transects totalling 100 km were located within a 40-km radius; in the small reserve, there was one 17.6 km route. The counts were done twice each autumn at 8-10 day intervals, and the density figures were averaged. The same routes were covered each year; they traversed forest types in proportion to their general occurrence in the reserves (Table 1). Within forest types, routes were located at random with regard to grouse habitat.

Since 1973, numbers of carnivores and Capercaillie have been estimated in the small reserve during late February/early March each year when the ground was covered with snow. A similar count was started in the large reserve in 1979 and in the logged area outside the small reserve in 1988. The survey areas within the small reserve and the logged area were chosen so that they closely resembled each other in site quality (forest type) composition. The counts were done by single men walking along the transect lines which formed a grid with 1 km between lines (1 x 1 km square). The grid (survey area) covered an area of 1,254 ha in the large reserve, 642 ha in the small reserve and 756 ha in the logged area, making the total length of lines 209 km, 107 km and 126 km respectively. Ten to twelve observers, each walking approximately 10 km, made the survey twice, with one day between counts. On the first day, Capercaillie within 30 m on both sides of the lines were counted and all carnivore tracks that crossed lines within the grid were covered with snow. On the next day, all new tracks that crossed lines within the grid were marked on maps. Densities of carnivores were estimated by comparing maps and counting the numbers of tracks that ended within each square of the grid.

During the years 1976 to 1985, data on clutch sizes, hatching date and number of chicks in broods throughout the summer were collected on Capercaillie within the small reserve, partly through systematic searching and partly by reserve personnel doing their daily work in the reserve. Single hens without broods were not recorded. Since 1980, dispersal of sub-adult grouse has been studied from recapture and hunter reports of leg-ringed birds. The birds were live-trapped when visiting dustbowls in autumn. Distance of dispersal was measured for birds marked during August and recaptured or shot during October or later (Swenson 1991). Abundance of small rodents in the large reserve was determined from no less than 10,000 trap nights during the summer each year. Traps (boxtraps for catching squirrels alive) were baited with mushrooms and left unset throughout the summer.

We used Student's analysis of variance to test for differences in animal densities. Correlation and regression analyses were used to test for synchrony between population parameters and population fluctuations and for trends in recorded bird densities over time. To test whether the populations fluctuated in a cyclic manner, we used a correlogram combined with a correction for long term trends in bird densities (Kendall 1973).

Results

Grouse density and population fluctuation

The Hazel Grouse was the most abundant species along the transect routes of the spruce-dominated large main reserve, while Capercaillie dominated along the routes through the pine forests of the small reserve (Figs. 2 and 3). The average late winter density of Capercaillie during 1988-93 was significantly lower in the logged forests surrounding the small reserve (0.8 birds/km^2) than within the small reserve (2.8 birds/km^2) ($p<0.001$).

There has been a significant decrease in the autumn Capercaillie population of the small reserve ($r = -0.5$, $p<0.001$), while there has been no long term change in the population densities of Capercaillie and Hazel Grouse in the larger reserve ($r = -0.2$, $p<0.2$ and $r = -0.3$, $p<0.1$, respectively), nor in the Hazel Grouse population of the smaller reserve ($r = 0.1$, $p< 0.6$) (Figs. 2 and 3). The decrease in the Capercaillie population of the small reserve has not been gradual, but occurred as a crash in 1968. This Capercaillie population has not recovered since. The Hazel Grouse populations within both sections of the reserve and the Capercaillie population of the large reserve also underwent a temporary decrease during the years 1966-70 (Figs. 2 and 3).

Analysis of autocorrelation revealed no significant cyclicity in the population fluctuations of either species ($r < 0.30$). However, if the high count of Hazel Grouse in 1953 is excluded, there appears to be a cyclic rhythm in abundance with 8-9 years between peaks for this species within the large reserve. The population fluctuations were significantly synchronized between Capercaillie in the small and large reserves ($r = 0.5$, $p< 0.003$) and between Capercaillie and Hazel Grouse in the large reserve ($r = 0.3$, $p<0.01$). The Hazel Grouse of the small reserve fluctuated independently of the other populations.

Productivity

During the study period 1976-85, the average date of hatching of Capercaillie was 17 June with 8 and 24 June as extremes (n=146). The average number of eggs in clutches was 6.35 (S.E. = ± 0.4, n = 146). Hatchability was determined in 16 clutches spread over several years. Ten percent of the eggs failed to hatch. The average size of broods decreased over the summer from 4.6 (S.E. = ± 0.3, n = 33) in June and 3.6 (S.E. = ± 0.2, n = 62) in July to 3.5 (S.E. = ± 0.2, n = 61) in August. The main decrease in number of chicks occurred during the first 10 days after hatching.

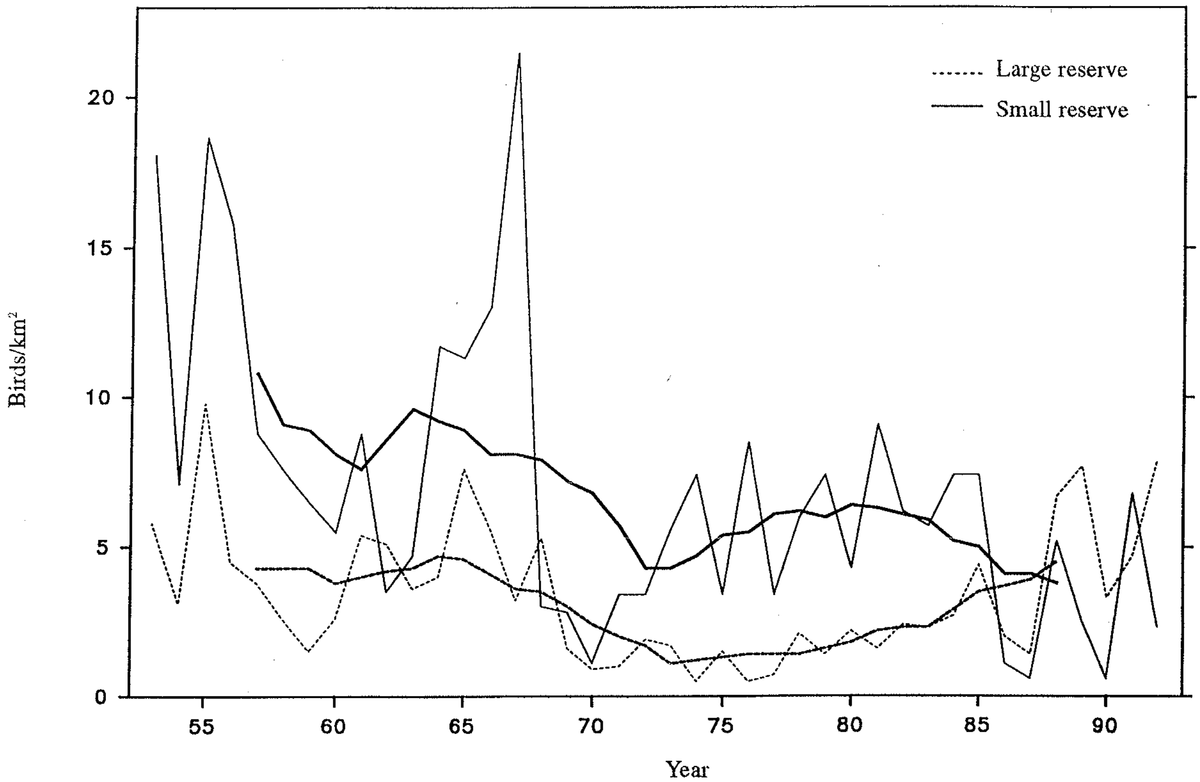

Fig. 2. Autumn densities (fine line) and nine-year moving average densities (thick line) of Capercaillie during a 40-year period in a small and large section of the Pechora-Illych Nature Reserve, North Ural, Russia.

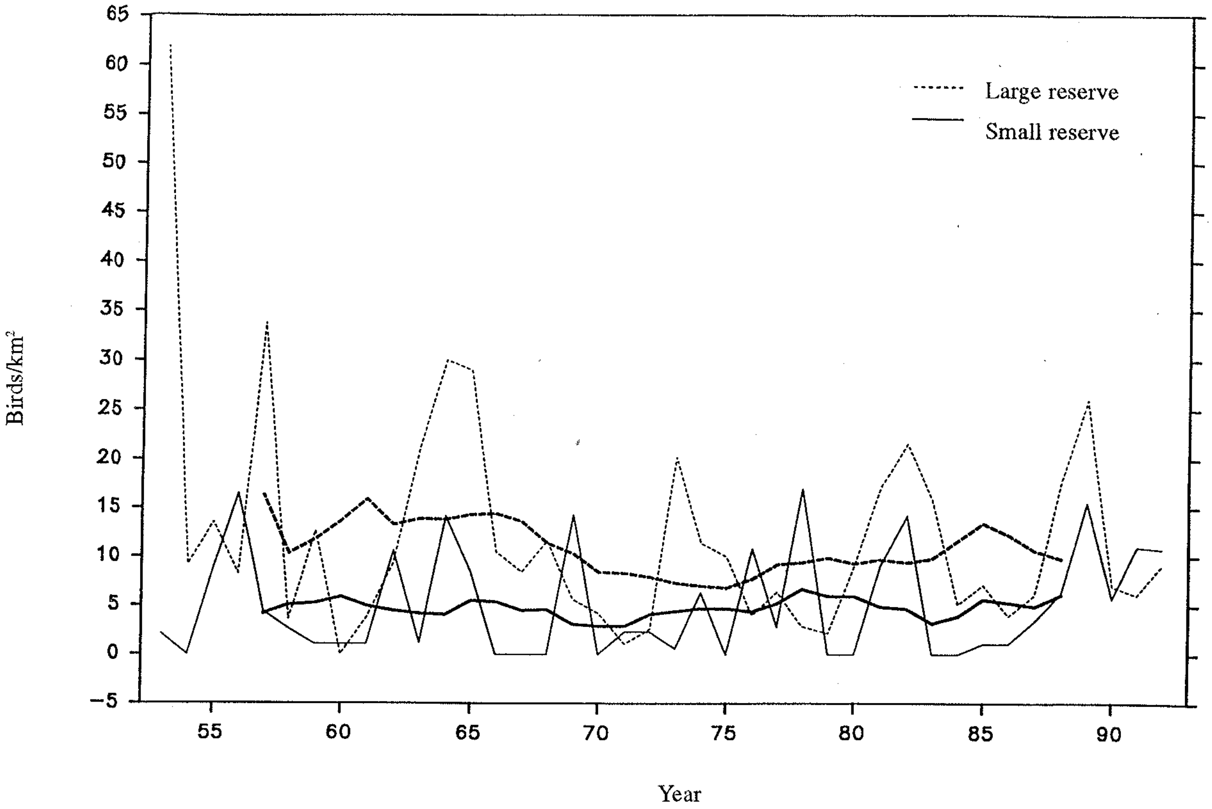

Fig. 3. Autumn densities (fine line) and nine-year moving average densities (thick line) of Capercaillie during a 40-year period in a small and large section of the Pechora-Illych Nature REserve, North Ural, Russia.

Dispersal

Average distance of dispersal was 5.2 km for female Capercaillie (n=18), 1.2 km for male Capercaillie (n=6) and 1.6 km for Hazel Grouse (both sexes combined)(n=10). Maximum distances of dispersal were 12, 2, and 5 km for female and male Capercaillie and Hazel Grouse, respectively. Four birds of all three species were shot or captured at least one year after marking. Dispersal distance was significantly different between female Capercaillie and both male Capercaillie and Hazel Grouse ($p<0.05$), but not between Hazel Grouse and male Capercaillie ($p>0.05$). For the period 1976 to 1985, the proportion of males to females in winter counts of Capercaillie within the small reserve was approximately 1:1 (50.2 %, S.E. = ± 1.4), but the proportion of males varied between years from 36 - 62 %.

Density and fluctuations of carnivore

Density indices of red fox and mustelids did not differ significantly between the small reserve and the logged forest (Fig. 4), and there has been no significant change in the indices within the small reserve during the period of intensive logging (beginning in the early 1970s) of surrounding forest ($r=0.1$, $p>0.6$).

Abundance of red-backed voles *Clethrionomys glareolus* and red voles *C. rutilus* in the large reserve fluctuated in a cyclical manner with 4-5 years between peaks ($r=0.6$, $p<0.01$). Density indices of stoats also showed a cyclical pattern with a periodicity of 4 years (Fig. 5). Stoat abundance increased during successive years of rodent abundance and peaked at the end (crash year) of each rodent cycle (Fig. 5). There was no cyclicity in density of pine martens *Martes martes* within the large reserve ($r<0.02$, $p>0.05$) and pine marten abundance showed no relationship to the rodent cycle. However, the proportion of juveniles in the yearly catch of pine martens fluctuated between 80-90% during peak rodent years and 20-25% when rodents were scarce (Pechora-Illych research station, unpublished material). Foxes were rare within the large reserve. There was no correlation between the fluctuations of rodents and stoats and the autumn numbers of Capercaillie and Hazel Grouse ($r<0.3$, $p>0.05$). Nor were there any correlations between brood size in August (females without broods excluded) and rodent/stoat numbers ($r<0.3$, $P>0.05$).

Discussion

Finnish grouse populations have been monitored since 1963 using the same route transect method as in this study (Rajala 1974). As the Finnish forests are subjected to modern, industrial forestry, it is particularly interesting to compare Finnish grouse populations with those of the undisturbed forests of the Pechora-Illych reserve. We have utilized results from central Finland for comparison, because this region represents continental boreal forest at the same

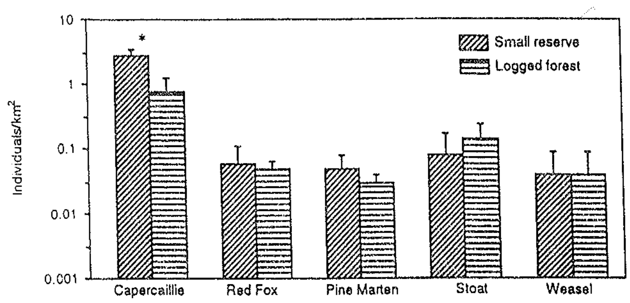

Fig. 4. Estimated densities of Capercaillie, red fox and mustelids in late February - early March in undisturbed forest (small section, Pechora-Illych Nature Reserve), compared to surrounding logged forest, North Ural, Russia, 1988-93.

Logarithmic Y-axis; vertical bars show standard deviation.
* = significant difference ($p<0.0001$) in density between reserve and logged forest.

latitude and with generally the same tree composition as in our study area.

In the Finnish surveys, observers are asked to plan their routes so that they follow the best grouse habitats (Rajala 1974, Lindén and Rajala 1981), but to what extent this is done is questionable. The Finnish transects therefore may better be regarded as representing random routes including areas of poor Capercaillie habitat such as clear cuts and young forest (Lindén pers. comm.). In the Pechora-Illych reserve, approximately 70% of transect lengths were in forests older than 80 years (Table 1). Therefore prime Capercaillie habitat may be under-represented in the Finnish surveys compared to those of the Pechora-Illych reserve.

Grouse density and population changes

During the years 1953-68, the average recorded number of Capercaillie in the transect belt of the small reserve was 10.3 birds/km², decreasing to 4.8 birds/km² for the years 1969-93. These density figures are similar to those reported for the Finnish route counts (Rajala 1974, Lindén 1989, Lindén et al. 1990). In the best habitats of central Finland, the mean population density of Capercaillie was 15-16 birds/km² during the years 1963 to 1966, decreasing to approximately 4-6 birds/km² during the 1980s. The highest Capercaillie densities in Finland were found in the province of Vaasa, where average density figures were around 20 birds/km² in the mid-1960s, but here also density figures decreased to 4-6 birds/km² during the 1980s.

At Pechora-Illyich, all four grouse populations within the reserve decreased from the mid 1960s to the mid 1970s (Figs. 2 and 3), but only the Capercaillie population of the small reserve has failed to regain its former numbers. In 1971, a similar decrease with no subsequent recovery was recorded in Willow Grouse *Lagopus lagopus* by Myrberget on Tranøy, Northern Norway. This population was reduced to one-third of its former size due to nest failure and has not recovered subsequently (Myrberget 1984). In both the large and the small reserve, the periods of high average Capercaillie density also show great differences between peak and low years (Fig. 2). Such large fluctuations also appeared characteristic for Norwegian Capercaillie populations before the Second World War when bird densities were, on average, much higher than today (Hjeljord 1980).

We do not know the former densities of Capercaillie in the areas surrounding the small reserve prior to logging, but the similarity in site quality and forest types between the two areas indicates similar carrying capacity. We therefore believe the low Capercaillie density in this area to be mainly due to logging. This is supported by the well documented

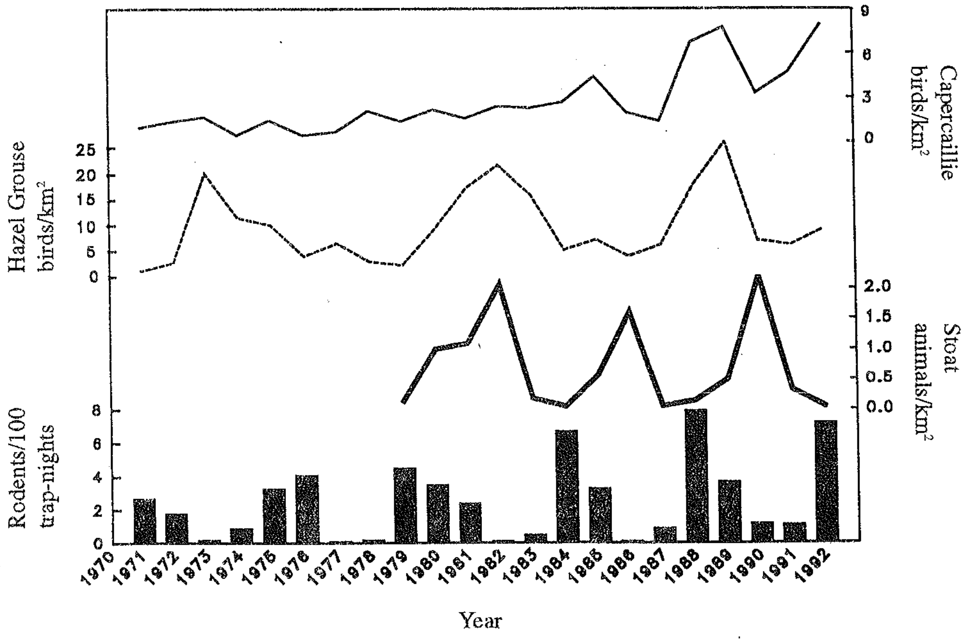

Fig. 5. Fluctuations in autumn densities of Capercaillie and Hazel Grouse compared to fluctuations in late winter densities (late February - early March) of stoats and summer abundance of rodents (*C. glareolus*), large section, Pechora-Illych Nature Reserve North Ural, Russia.

dependence of Capercaillie on old forest (Angelstam 1983, Wegge et al. 1992). A similar reduction of density was reported for the Finnish route counts, when compass transects traversed clearcuts and young forest instead of only prime habitat (Rajala 1974).

Hazel Grouse seemed to maintain their numbers in both sections of the reserve and were also the forest grouse that has shown the least decrease in Finland (Lindén and Rajala 1981, Järvinen and Väisänen 1984, Helle and Helle 1991). In the best Hazel Grouse habitats of central Finland, densities generally varied between 5 - 15 birds/km^2, compared to an average of 13.2 birds/km^2 (1953-93) in the large section of the Pechora-Illych reserve and 5 birds/km^2 in the small reserve.

Cyclicity of grouse numbers

According to the alternative prey hypothesis, periodic declines in populations of small rodents would be expected to cause cycles in the grouse populations (Hagen 1952, Angelstam et al. 1985). However, neither the autumn populations of Capercaillie and Hazel Grouse nor the brood size of Capercaillie showed any cyclicity synchronized to that of small rodents. This supports findings by Kastdalen and Wegge (1991) that chick survival of grouse may vary independently of the rodent cycle. There were no 6-7 year cycles in the Russian grouse like those of the Finnish grouse populations (Lindén 1989). If the Pechora grouse populations are cyclical, our data indicate a cycle length around 8-9 years. Our study represents a small sample from grouse populations of the upper Pechora region. Population data from a larger area are probably needed in order to detect cycles similar to those of the Finnish grouse populations.

Productivity

Average clutch size (6.35) and brood size in August (3.5) of Capercaillie in the reserve were smaller than reported from Central Finland (7.0 and 4.3, respectively) (Rajala 1974, Lindén 1989). However, because we do not know the number of females without broods in the Pechora-Illych reserve, we are not able to compare average productivity between the populations. But correcting for differences in clutch size, chick loss over the summer does not appear to have differed greatly between the undisturbed forests of the small reserve and the exploited forests of Central Finland.

Predation and dispersal

The depression of all four grouse populations around 1970 happened before intensive logging began in the region and was probably unrelated to human activity. Today, the small reserve is an island of undisturbed habitat within vast areas of logged forest, and we believe this to be the ultimate reason for the lack of build-up (rather a decreasing trend) of the Capercaillie population of this reserve. With habitat on the reserve unchanged, the most likely causes of failure to increase to former levels may be either increased predation or a net dispersal of birds out of the reserve.

Following logging of Scandinavian forests, a shift in the composition of the vertebrate fauna leading to higher density of small and medium sized carnivores has been suggested (Storaas and Wegge 1985, Henttonen 1989). Our data indicate no such effect for the north Russian taiga, and the lack of correlation between rodent and grouse cycles does not point to predation from mustelids as a strong over-riding factor in the dynamics of these grouse populations. A potential predator on grouse eggs, the Hooded Crow *Corvus cornix*, has increased in numbers in the upper Pechora region during recent years (Pechora-Illych Research Station unpublished material), but we have no data on the effect this may have on the grouse populations. The Golden Eagle *Aquila chrysaëtos* is an important predator on adult Capercaillie in this area but is less important for Hazel Grouse (Pechora-Illych Research Station unpublished material). Increased predation from Golden Eagles within the reserve due to the attraction of high prey density, therefore, could be one reason why the Capercaillie has been less able than the Hazel Grouse to maintain its population level.

The dispersal of ringed birds supports earlier studies showing female Capercaillie making longer movements than male Capercaillie and Hazel Grouse (Swenson 1991, Wegge et al. 1992). This could be one reason for the difference in population trends between Capercaillie and Hazel Grouse within the small reserve. A net export of females out of the small reserve could also help explain why there is an even sex ratio of Capercaillie within the reserve in contrast to the female biased ratios commonly reported for larger areas of managed forest in Scandinavia (Rajala 1974, Wegge 1980).

Conclusion

Available data on density and dynamics of Capercaillie populations at the Pechora-Illych reserve do not indicate substantial differences from those reported for Capercaillie populations of managed Scandinavian forests. However, to understand the causes underlying the long term changes of the grouse population in this reserve, more comprehensive studies are needed. In particular, we need more information on recruitment and on dispersal out of the reserve. In the general context of Capercaillie conservation, it appears important to know why a Capercaillie population in north Russia has declined in a large area (20,000 ha) of natural habitat although this was not disturbed by human activities.

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Summary

We report yearly fluctuations in numbers over the last 40 years of Capercaillie and Hazel Grouse in large virgin forests of north Ural. Over a shorter period, we also compare densities of Capercaillie and carnivores in logged and protected forests and we have collected data on population dynamics of Capercaillie and on dispersal of Capercaillie and Hazel Grouse. Densities of Capercaillie and Hazel Grouse were similar to densities of these species in Scandinavian forests. Within a protected reserve of 20,000 ha, Capercaillie populations have decreased, while in a large area of virgin forests, Capercaillie have maintained their numbers. Hazel Grouse maintained numbers within both the small and large areas of protected forest. No differences in densities of red fox and mustelids were recorded between logged and protected forests, and there has been no change in abundance of these predators within the 20,000 ha reserve since the start of intensive logging of surrounding forests. Female Capercaillie made longer dispersal movements ($\bar{x}$ = 5.2 km) than male Capercaillie and Hazel Grouse ($\bar{x}$ = 1.2 km and 1.6 km, respectively), but at present we cannot explain the differences in population trends between Capercaillie and Hazel Grouse in the 20,000 ha reserve which was not disturbed by human activities.

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Extrinsic factors influencing the population dynamics of Red Grouse *Lagopus lagopus scoticus*

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Introduction

The population dynamics of Red Grouse *Lagopus lagopus scoticus* vary both temporally and spatially, even within the birds' relatively small geographical range of heather moorland in Britain. Both intrinsic and extrinsic mechanisms have been shown to play some part in the population processes that influence breeding density and breeding production (reviewed by Lawton 1990). This paper concentrates solely on extrinsic factors, in particular the impacts of parasitism and the interaction between parasitism and predators. Detailed population data coupled with intensive radio-tracking, field experiments and detailed mathematical modelling have described the roles of these different factors on the population dynamics of Red Grouse. This paper summarises these findings.

Red Grouse have been killed as game on private sporting estates in Britain for several centuries. Intensive grouse management and driven grouse shooting started in the middle of the 19th Century. Many of these sporting estates keep detailed daily and annual records of the numbers of grouse shot and have done so for more than 100 years, thus providing a detailed description of changes in the abundance of the birds both spatially and temporally. Most of these time series data exhibit statistically significant cyclic fluctuations in numbers (Potts et al. 1984, Hudson 1985, Hudson 1986a), although bag records from estates in Scotland have also shown marked longterm declines over the last 40 years (Hudson 1992). Populations of grouse in the north of England tend to show five-year cycles (Potts et al. 1984) and the frequency of the cycles increases to around 10 years in the north of Scotland (Hudson 1992). Grouse populations which show no statistically significant tendency to cycle are located either on the dry freely drained areas of heather moorland in the east of the country or are on relatively small areas of moorland (Hudson 1992).

Red Grouse and the caecal nematode *Trichostrongylus tenuis*

Life cycle

The parasitic nematode *T. tenuis* has a direct life cycle with no intermediate or alternative hosts. The adult parasites live in the caeca of Red Grouse and produce eggs which are passed by the host with the daily excretion of caecal faeces. Eggs hatch within the faeces and produce larvae which migrate to the tips of the heather plant where they are ingested by feeding grouse. Ingested larvae develop into adults but they may enter a period of arrested development known as hypobiosis (Gibbs 1986, Schad 1977). The cue for whether or not they enter hypobiosis is likely to be temperature dependent. In the north of England, there are two main periods of infection, one during late summer and a second in early spring when only a small proportion of parasites enter hypobiosis. Further north in Scotland, hypobiosis seems to occur amongst a higher proportion of the worms and may last for longer. The dynamic consequences of this are explored by Dobson and Hudson (1992).

Young grouse are uninfected with parasites when they hatch and steadily accrue an increasing burden of parasites as the proportion and quantity of heather shoots in their diet increases. The pattern of worm distribution changes with age of the grouse from a random distribution to an aggregated distribution described by the negative binomial distribution (Hudson 1986a, 1992). There is no difference in either mean worm burden or the pattern of distribution between male and female birds, although mean parasite burdens in a population may vary between 100 worms per bird to 10,000 worms per bird (Hudson et al. 1992b).

Effect of parasites on host survival and fecundity

Experimental studies which compared the fecundity and survival of grouse treated with anthelmintics with that of untreated birds carrying natural levels of infection demonstrate that the parasite has a more pronounced effect on host fecundity than it does on host survival (Hudson 1986b, Hudson et al. 1992b). The basic technique used was to fit female grouse at the beginning of the year with radio transmitters, and to treat alternate birds with an anthelmintic drug (Levamisole) to reduce parasite burdens. Control birds were given water instead. The birds were then followed throughout the course of the following breeding season and clutch size, hatching success and chick production were measured as indices of reproductive success. In each year, the breeding production of the treated birds, which had few parasites, was consistently lower than that of the control birds which had natural parasite burdens (Fig. 1). Statistically significantly differences were detected in clutch size, hatching success, and in numbers of chicks surviving to 10 days and 3 months (Hudson 1986 b, Hudson et al. 1992b).

This experiment also provides an estimate of the effects that worm burdens have on grouse survival because control and treated birds were recovered in each year that the experiment was performed. These data can be combined with data on the year to year fluctuation of numbers in grouse on our principal study site to provide an estimate of parasite impact on host fecundity and mortality (Hudson et al. 1992b). The

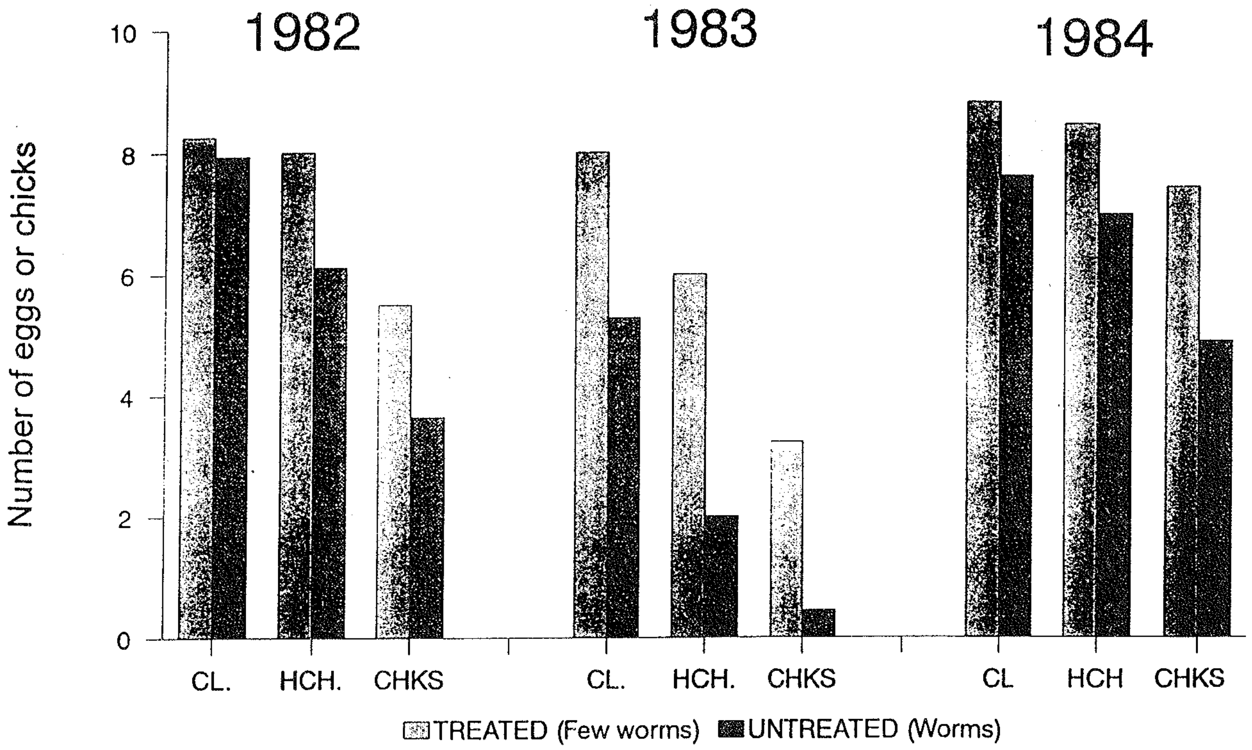


Fig. 1. Comparison of the breeding production of Red Grouse in three years of treatment where 1983 was a year of high parasite burdens during which treatment of hens significantly increased clutch size (CL.) hatching success (HCH.) and number of chicks produced (CHKS) (after Hudson 1992b). Comparative results for 1982 and 1984 are also presented.

parasite had a larger effect on fecundity than on survival, a characteristic which when combined with the low degree of aggregation of the parasites in the host population may have caused the system to cycle (May and Anderson 1978, Dobson and Hudson 1992).

Mathematical models for *T. tenuis* and Red Grouse

The basic Anderson and May (1978) model for host-parasite inter-relations for direct life cycle macro-parasites may be adapted to examine the population biology of *T. tenuis* in Red Grouse. The differential equation framework used in this model acknowledges that the dynamics of the parasite operate continuously. Although discrete frameworks are more commonly used for models that only consider the dynamics of bird populations, the disparities in temporal scale between the dynamics of the parasite and those of the host require us to use a model framework that can examine processes that occur at a mixture of different rates. We have modified the Anderson and May (1978) model by adding additional equations that examine the dynamics of the free-living stages and the arrested larval stages. The model therefore consists of four coupled differential equations describing changes in the number of the hosts, *H*, adult parasites, *P*, free living larvae, *W*, and arrested larvae, *A*.

$$dH/dt = (a - b)\,H - (\alpha + \delta)P \quad (1)$$

$$dW/dt = \lambda P - \gamma W - \beta WH \quad (2)$$

$$dA/dt = \sigma\beta WH - (\mu_A + b + \theta)\,A - \alpha\frac{PA}{H} \quad (3)$$

$$dP/dt = \theta A + (1 - \sigma)\,\beta WH - (\mu_P + b + \alpha)\,P - \alpha\frac{P^2}{H}\left(\frac{\kappa+1}{\kappa}\right) \quad (4)$$

The parameters of the model are described in Table 1, and correspond to the birth and death rates of the parasite and host at each stage of their life cycles. The model assumes that a proportion of larvae, a, enter arrestment for a constant period of time, $1/\theta$.

This model has similar structure and properties to the basic Anderson and May direct life cycle helminth model with a number of small but significant differences (Anderson and May 1978, May and Anderson 1978). The interaction between the parasites and the host will be stable if the parasites are aggregated in their distribution ($\kappa < 2$) and if the per capita impact of the parasites on host survival exceeds its impact on host fecundity ($\alpha > \delta$). The experiments described above suggest that neither of these conditions is frequently met in the *T. tenuis* Red Grouse system (Hudson et al. 1992b, Dobson and Hudson 1992). Instead, experiments have shown the parasite to exhibit greater impacts on host fecundity than on host survival and the degree of parasite aggregation, although significant, are relatively low. Interactions between these two processes is sufficient to produce cycles in the abundances of parasites and hosts and these are the primary mechanisms responsible for cycles observed in Red Grouse populations in the North of England. The addition to the model of expressions for the free-living and arrested larval stages of the parasite modifies the behaviour of the model: the presence of cycles is now also dependent upon the growth rate and survival of the free living larvae. The life expectancy of the free-living stages is crucial in determining whether or not the parasite can establish. In contrast, increases in the duration of larval arrestment tend to stabilise the system and can lead to stable numbers of parasites and hosts (Fig. 2). Equations 1-4 can be used to derive an expression for the growth of the parasite population when first introduced to the host population. This produces an expression for the basic reproduction ratio of the parasite, R_0, i.e. the number of breeding female worms in the next generation which an adult female worm produces in her lifetime (Dobson and Hudson 1992).

$$R_0 = \frac{T_1}{M_1 M_2} \left[(1 - \sigma) + \frac{\sigma \theta}{M_3} \right] \qquad (5)$$

The expression consists of a 'birth' term, $T_1 = \beta\lambda H$, the rate of transmission of eggs from birth through to establishment in another grouse, and the mortality rates ot each stage in the life cycle: adult worms, $M_1, = (\mu_P + b + \alpha)$, free-living larvae, $M_2 = (\gamma + \beta H)$, and arrested larvae, $M_3 = (\mu_A + b + \theta)$ This can be rearranged to give an expression for the threshold density of hosts, H_T, required to sustain continuously an infection of *T. tenuis* (Dobson and Hudson 1992).

$$H_T = \frac{\gamma M_1}{\beta(\lambda[(1 - \sigma) + \frac{\theta\sigma}{M_3}] - M_1)} \qquad (6)$$

These expressions quantify the effect of life expectancy of free-living larvae on the basic reproductive rate of the parasite and the threshold density of hosts required for the parasite to establish. As larval life expectancy decreases ($1/\gamma \Rightarrow 0$), R_0 the basic reproductive ratio of the parasite falls below unity and the parasite is unable to establish. The expressions also illustrate the effect of larval arrestment on the ability of the parasite to establish; as the proportion of larvae arresting increases, or as the duration of arrestment increases, either higher densities of the hosts, or increases in larval survival, are required for the parasite to establish.

The definitive experiment to demonstrate the importance of parasites is to remove (or reduce) worm burdens and show that the cycles die out. This experiment is being undertaken at a number of sites in the North of England. These current experiments show that treating birds with anthelmintic grit leads to a reduced tendency of grouse populations to cycle.

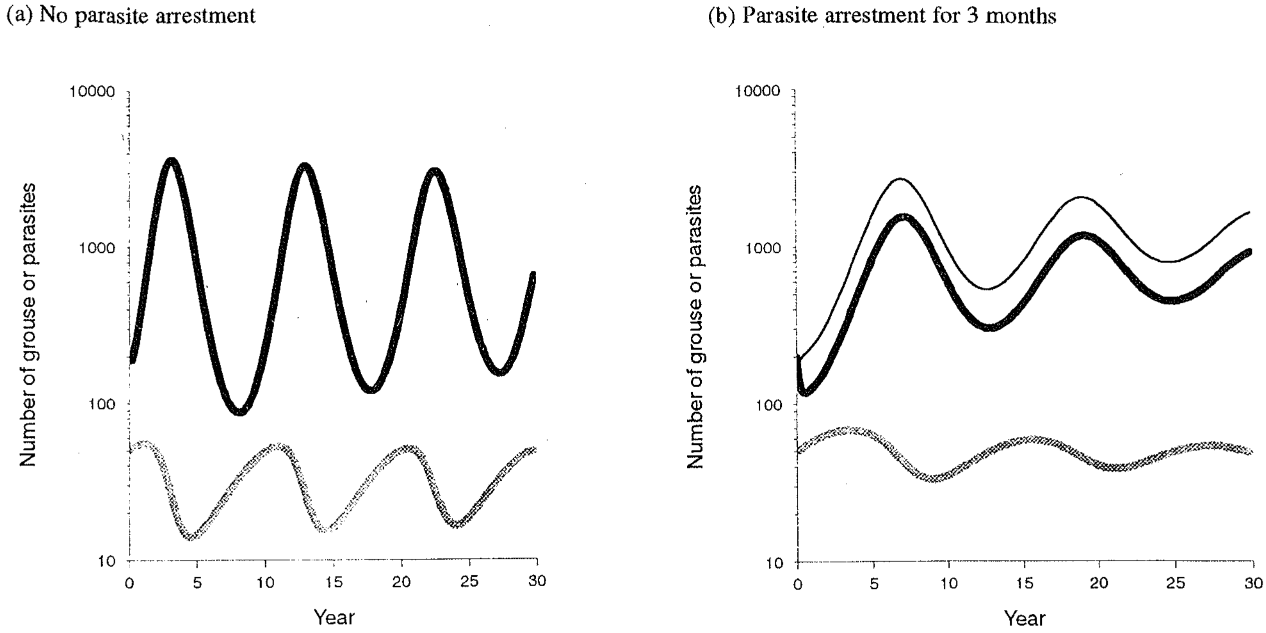
Red Grouse and their predators

Predators and predator control have been a traditional focus of game management in Britain. Information on mortality of Red Grouse from predation was obtained by monthly searches of the study area and the retrieval of all corpses found killed by predators. Information on predator abundance was obtained from direct observation or indirectly from the numbers of foxes and crows killed by keepers. Records of numbers of predators killed can be expressed either as the number of predators killed per unit area of moorland or as the number of predators killed per gamekeeper. The data have to be treated cautiously, as neither method provides an exact estimate of predator pressure. However, both are useful for illustrating trends in the numbers of predators in different geographical areas. Furthermore, as neither crows nor foxes lived exclusively on grouse or in moorland habitats, additional biases may occur in the numbers when expressed per unit area of moorland. These biases are further compounded by keepers who include in their totals of predators killed animals trapped or shot on neighbouring land under their control which is not grouse habitat. Similarly, the number of predators killed per keeper may not be a good reflection of predator pressure; few foxes, for example, may be killed either because few foxes are present or, alternatively, because little effort is made to control fox numbers.

Table 1. Parameter definitions and estimates used in the mathematical models. Derivation of the parameter estimates for the parasite and grouse are discussed in Hudson et al. 1992b and Dobson and Hudson 1992.

Parameter	Symbol	Estimated value (range)
Grouse fecundity	a	1.4 (0-2) /year.
Grouse mortality	b	1.05 /year.
Parasite fecundity	λ	11 (9.2-11.5) /year.
Adult worm mortality	μ_P	1.0 (0.8-1.2) /year.
Arrested larvae mortality	μ_A	0.5 /year.
Mortality of free-living parasite stages	γ	6.5-13 /year.
Duration of arrestment	$1/\theta$	2-6 months.
Proportion of larvae that enter arrestment	σ	variable between 0 and 1.
Parasite pathogenicity	α	3×10^{-4} /worm/year.
Parasite reduction in host fecundity	δ	5×10^{-4} /worm/year.
Aggregation of parasites in hosts	κ	1.0 (0.5-1.8).
Transmission rate	β	0.11 ($0.6-1.5 \times 10^1$)/larvae/host/year.
Transmission constant	H_0	60-120 (_/ß)
Predator rate	δ	100/grouse/year.
Parasite-induced increase in susceptibility to predators	π	1×10^{-3}/parasite.
Density dependent reduction in grouse breeding success	W	0.0003-0.03/grouse/year

Fig. 2. The transient dynamics for the model described in equations 1-4. Each figure shows numbers of grouse (lowest line) and adult worms (thick black line) and describe (a) the dynamics with no larval arrestment and (b) the dynamics with the presence of a three-month larval arrestment; total numbers of worms and arrested larvae are shown by the thin black line (Dobson and Hudson 1992).


(a) No parasite arrestment

(b) Parasite arrestment for 3 months

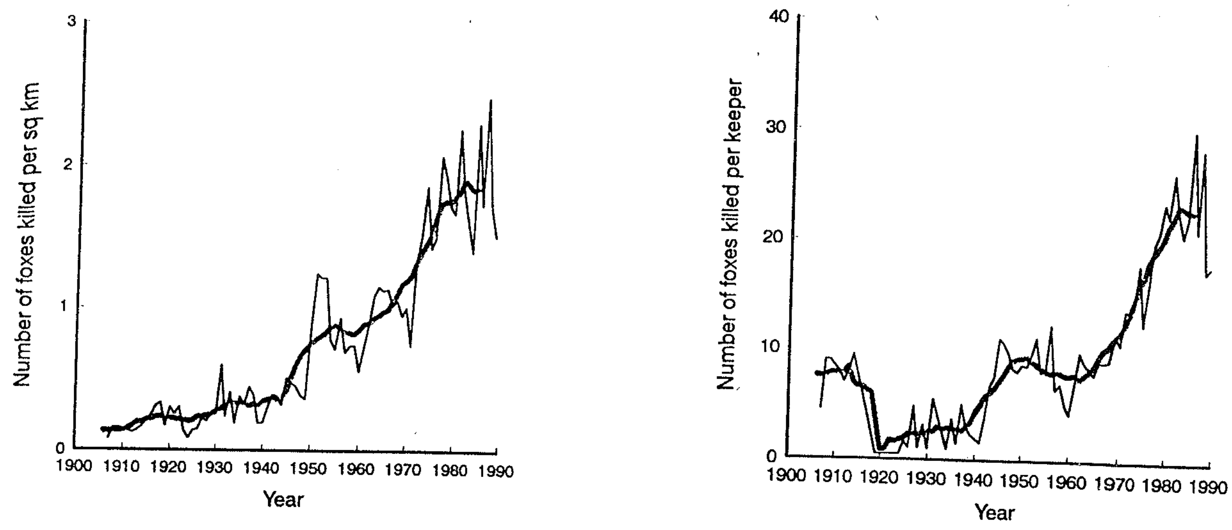
The numbers of foxes killed per gamekeeper and per unit area have increased on managed Scottish grouse moors particularly since the second World War and the end of the 1960s (Fig. 3). In Scotland, the number of foxes killed per square kilometre doubled from the 1960s to the 1980s, averaging at about two per square kilometre in the early 1980's. Scottish keepers killed consistently more foxes than English keepers, probably because there are fewer keepers per unit area. On average, a Scottish keeper killed 23 and an English keeper 13 foxes per annum. The increase in fox numbers in Scotland coincided with the beginning of the recent decline in numbers of Red Grouse in southern and eastern Scotland and may be a factor that prevented grouse numbers from increasing in the 1980s (Hudson 1992).

One way of examining the impact of foxes on grouse densities is to do a controlled experiment where one area has no fox control and a second comparable area has fox control. While no randomised experiments have been conducted there are a number of cases of changes in estate management where grouse bags have increased dramatically following the implementation of either fox or crow control (Hudson 1992). One good example occurred on two moors on northern England, both of c. 17 km^2 on opposite sides of a valley where the bag records fluctuated in parallel prior to changes in management. On one of the moors the level of fox control decreased following illness of the keeper (Fig. 4). The reductions in fox control were followed by significant declines in grouse numbers which remained so low that more foxes than grouse were killed during the first grouse shoot. Grouse numbers remained low until the sick keeper was replaced with an active keeper who removed the foxes. Numbers of grouse then recovered and the population regained its propensity to cycle, though it was now out of phase with the population on the other side of the valley. These results are consistent with results from the Game Conservancy Trust's research on the Salisbury plain in England where predator numbers were controlled in a strictly experimental manner (Potts and Aebischer 1991).

Table 2. Numbers of nests of Red Grouse found by dogs (scent) and random search (researchers) with respect to treatment of the female with an anthelmintic to reduce parasite burdens. The results show that dogs found a significantly larger proportion of infected birds suggesting that infected birds emitted more scent and were more vulnerable to predators (after Hudson et al. 1992a).

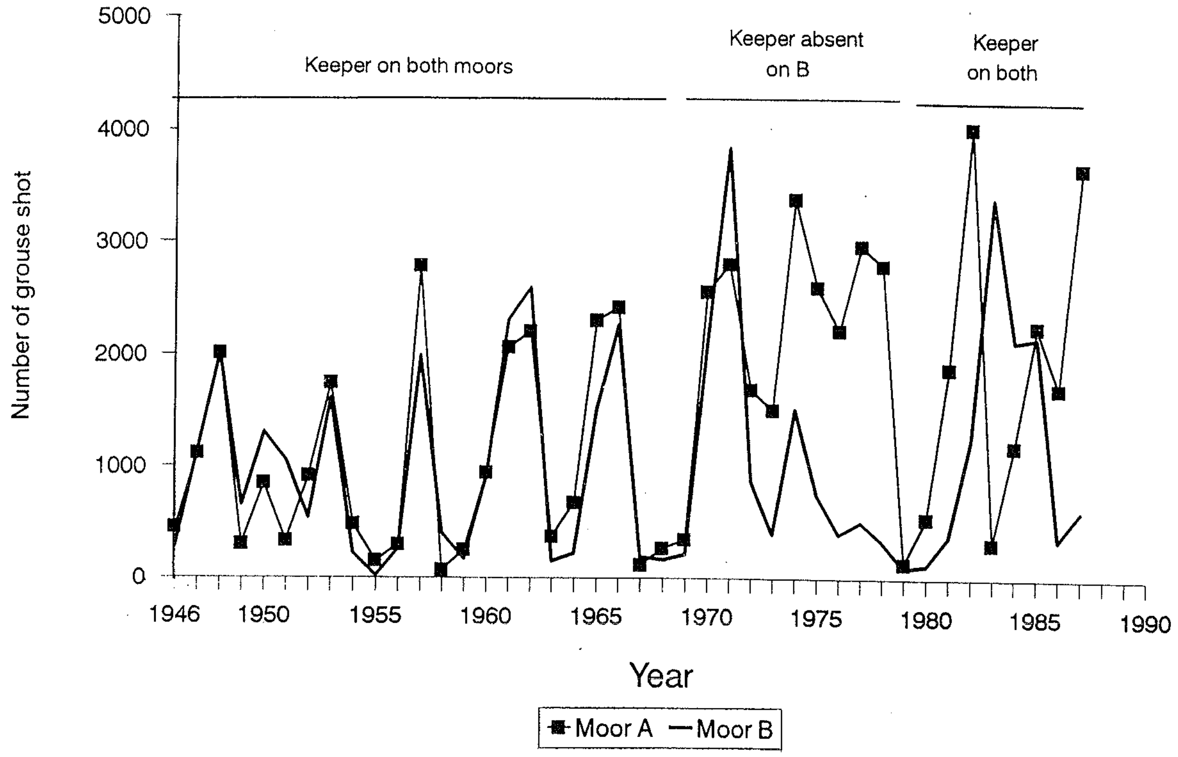
Year	Treatment	No. of nests found	
		Scent Dogs	Random search Field workers
1983			
Females treated	Low worm burden	6	7
Females untreated	High worm burden	37	10
1984			
Females treated	Low worm burden	9	7
Females untreated	High worm burden	29	7

Fig. 3. The numbers of foxes killed on Scottish grouse moors in this century expressed as (a) numbers killed per square kilometre of moorland and (b) numbers killed per keeper (after Hudson 1992). The fine lines are annual estimates and the thicker line the 10 year running mean.


(a) Numbers of foxes killed per unit area in Scotland

(b) Numbers of foxes killed per keeper in Scotland

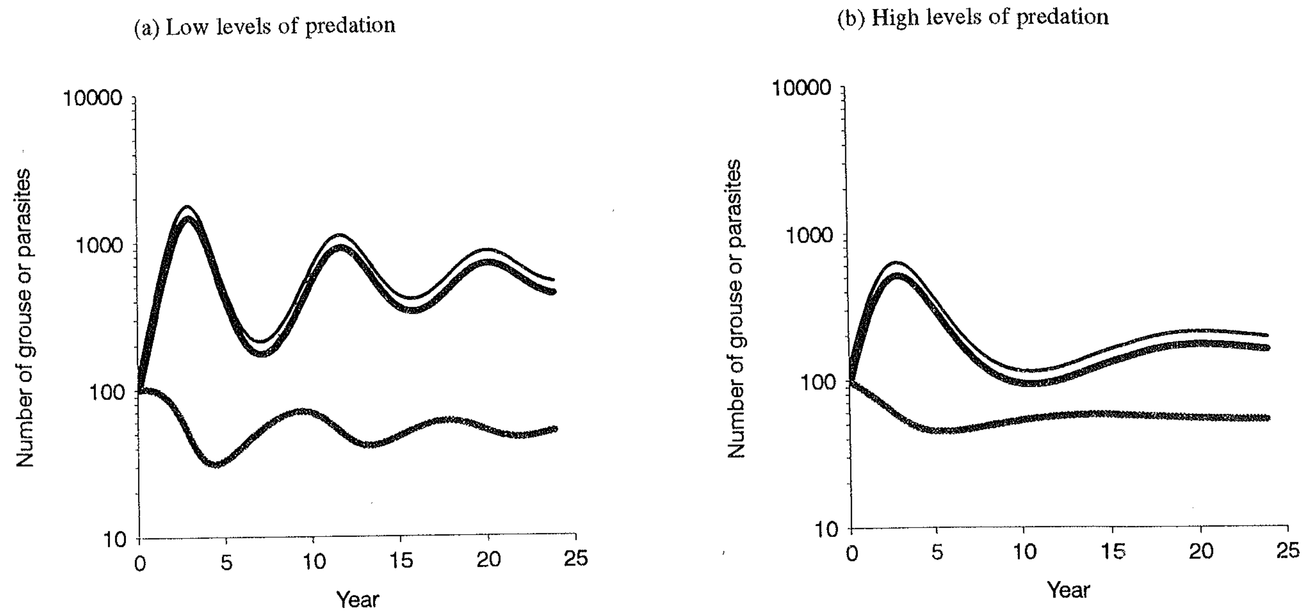
Fig. 4. The numbers of grouse shot on two adjacent moors in the north of England, one with an active keeper present throughout (Moor A) and one with a keeper absent for a period (Moor B). On Moor B, the keeper was ill for a number of years but was replaced after 1980.



Interactions between predators and parasites

Like many ground nesting birds, grouse are particularly vulnerable to predators when incubating and show various adaptations to avoid capture. For most of the year, the birds emit scent which can be detected by a trained pointing dog at distances of up to 50 m. Female Red Grouse stop producing caecal faeces during the spring incubation period and dogs can only locate incubating females from a distance of less than 0.5 m (St John 1878). This reduction in scent emission is associated with a change in the function of the bird's caeca that appears to be an adaptation to reduce detection. The par-

Fig. 5. The long term dynamics of a model where both predators and parasites are dependent on grouse abundance but at two levels of predator, (a) with 2 foxes and (b) with 10 foxes present. The presence of a predator tends to dampen the cycles and higher levels of predators to reduce the average number of grouse shot.


(a) Low levels of predation

(b) High levels of predation

asitic nematode *Trichostrongylus tenuis* is known to burrow deeply into the caecal mucosa causing disruption of the plicae and bleeding (Watson et al. 1987). This pathology may hinder the control of scent emission and so increase the susceptibility of heavily infected incubating birds to mammal predators that hunt by scent.

We have experimentally examined the role that parasites play in increasing the susceptibility of grouse to predators (Hudson et al. 1992a). The experiment used trained dogs to locate the nests of grouse and demonstrated that incubating female grouse with reduced parasite burdens were less likely to be found than control birds with natural infections (Table 2). Although the physiological mechanism controlling the emission of scent is not understood, female Red Grouse with high worm burdens were found to have relatively large caecae which may have emitted more scent during incubation. An alternative possibility is that the parasites compete for the female's reserves during incubation so that the female leaves the nest more frequently and this results in more scent being left near the nest of heavily parasitised females. In either case, the presumption is that the presence of parasites makes incubating females more vulnerable to predators.

Dynamics of predation and parasitism: mathematical model

The mathematical models described above can be modified to include the effects of predators on Red Grouse and the resultant effects on the parasite and host populations. To undertake this, we first simplify our earlier model and assume that the dynamics of the free living larvae work on a fast time scale compared to the dynamics of the adult worms, arrested larvae or hosts. This allows us to collapse equation 2 into an additional term at the beginning of equation 3 by setting $H_0=\gamma/\beta$. The proportion of free-living larvae that successfully establish in hosts is thus $H/(H+H_0)$. The modified model that includes predators considers two cases: in the simplest case the parasites have no effect on the vulnerability of their host to the predator; in the second case, the susceptibility of the grouse to the predator increases with the intensity of the parasite burden.

The parameters are again described in Table 1; this modified model assumes that a constant number of predators, F, catch grouse at a rate r, while the per capita rate at which parasites increase the susceptibility of their hosts to the predator is p. When the parasites have no effect on the host's susceptibility to predators, then p and all the terms including p in equations (7),(8) and (9) are zero. The model assumes that the dynamics of the predator population are independent of the grouse and that predation rates increase with grouse density as a simple linear Type I functional response (Holling 1965).

In the simplest case, with no larval arrestment, the grouse population decreases as additional mortality due to predation

The dynamics of the model can be described using the following three equations:

$$dH/dt=(a-b)H-(\alpha+\delta)P-\rho HF-\pi\rho FP \quad (7)$$

$$dA/dt=\frac{\lambda PH}{H+H_0}-(\mu A+b+\theta+\rho F)A-\alpha\frac{PA}{H}-\pi\rho\frac{PAF}{H} \quad (8)$$

$$dP/dt=\theta A-(\mu P+\alpha+b+\rho F)P-\alpha k^1\frac{P^2}{P}-\pi\rho FH\left[\frac{P}{H}+\frac{P^2}{H^2}\kappa^1\right] \quad (9)$$

is added to the system (Fig. 5). In contrast, if the parasites enter a prolonged period of arrested development, then increased predation can lead to increases in the grouse population. This counter-intuitive result is due to the predators selectively removing a large proportion of the worm population before it has an impact on the host population. This reduces the net impact of the parasite on the grouse population and allows this to increase to a level determined by the combined effects of low predation and reduced parasitism. Further increases in the numbers of predators ultimately reduces the size of the grouse population and may drive the hosts below the threshold where they can sustain infection by the parasites. The levels of parasite-induced increases in predation observed in the grouse-*T.tenuis* system produce very little difference in the size of the host population when compared to the situation where the predator is acting at random.

The transient dynamics of the system are also influenced by the predator. Most importantly, the presence of predators reduces the tendency of the host and parasite populations to cycle (Fig. 5). This occurs principally because predators reduce parasite burdens by removing parasitised hosts from the population, reducing the delayed density-dependent effects of the parasite on host survival and breeding, and suspending the mechanism that generates the population cycles. This result is in accord with previous explorations of the properties of models of this type (May and Anderson 1978, Dobson and Hudson 1992). The propensity of helminth parasites and their host populations to oscillate is a function of the ratio of parasite-induced reductions in fecundity to their effects on survival. As this ratio gets larger, the tendency to oscillate increases. The parasite-induced increases in susceptibility to predation reduced the propensity of the system to oscillate by increasing rates of parasite-induced mortality.

The models can be further modified by explicitly considering the dynamics of the predators (Dobson and Hudson in litt.). These models can produce still further complexities in the long-term decline of grouse, predators and parasites. Under some conditions, these models can produce sustained limit cycles in the abundance of all three species. Under other conditions, the presence of an increasing density of predators leads to long term declines in parasite abundance.

Discussion

While studies in north-east Scotland have described the possible effects of intrinsic mechanisms on the density of Red Grouse (Watson et al. 1994), the work described here suggests that the long term dynamics of grouse populations can be determined by interactions with natural enemies such as parasites and predators. While predators are frequently the principle observed cause of mortality, parasitic helminths place a continuous energety drain on their hosts which causes morbidity, rather than mortality. Our studies suggest that this can lead to reduced fecundity and increased vulnerability to predators and thus have profound consequences for the population dynamics of the Red Grouse.

Overall, the data presented in Figs. 3, 4 and 5 suggest that the increase in numbers of foxes killed on grouse moors reflects an increase in the total population of foxes. This will have intensified predator pressure on grouse. Additional data on fox populations in Hewson and Kolb (1973), Kolb and Hewson (1980), and Hewson (1984) examine the numbers of foxes killed in the Forestry Commission areas and confirm that between 1961 and 1978 an increase occurred in the size of Scottish fox populations. When coupled with the recovery of birds of prey from the widespread use of DDT and control by game-keepers, there have probably been significant increases in predator pressure on grouse stocks in Britain over the past 20 years (for further details see Hudson 1992).

The increase in fox numbers could be a result of reduced control practices, or a change in the availability of food for foxes, or a combination of these factors. Although the biggest single decline in keeper numbers occurred in the 1940s, in the last thirty years there has been a steady reduction in the number of keepers employed in the management of Red Grouse. A major contributor to this decline occurred in the 1970's and 1980's when many grouse estates were sold to alternative land-use practices, usually commercial forestry. This led to further declines in the numbers of keepers within an area, and may also have resulted in increased numbers of foxes using the new forested areas as refuges. Foxes are generalists and will eat a wide range of food including sheep carrion, game and other species of wildlife. Numbers of sheep in most parts of Scotland have remained relatively stable, though the availability of sheep carrion has increased as changes in agricultural policy encourage quantity rather than quality in sheep flocks. Similarly, there has been an increase in number of red deer *Cervus elaphus* in Scotland, and presumably an increase in carrion from dead deer may provide food for foxes in winter. Nevertheless, the increase in fox numbers in much of southern Scotland where red deer are absent will not have resulted from this source of food.

The most obvious recent change in food for foxes was the increase in the number of rabbits *Oryctolagus cuniculus* following the recovery of their populations from myxomatosis in the 1950's and 1960's. The recovery of rabbits (as measured by numbers shot on both upland and lowland estates) showed a five-fold increase in the 1960's and 1970's; this coincided well with the increase in fox numbers during the same period but does not explain why fox numbers were low pre-myxomatosis when rabbits were plentiful. The increase of foxes probably results from a variety of conditions including keeper numbers being reduced to a level insufficient to control foxes and the rabbit population providing sufficient food to sustain high numbers of foxes. Interestingly, in England fox numbers did not increase even though rabbit numbers increased from the interim low level caused by the outbreak of myxomatosis in the 1950s. This was probably because there were sufficient keepers in England to control the foxes irrespective of the increase of rabbits.

All the above analyses suggest that interactions between Red Grouse and their natural enemies are crucial in determining the long term population dynamics of populations of this grouse species on upland estates in northern Britain. Traditional grouse management concentrated on predator control and habitat improvement. Only recently has the role of parasitic nematodes and other pathogens been brought into focus. In order to understand the role that parasites play in the population dynamics of Red Grouse we have attempted to develop a more holistic approach to the scientific inquiry and management of bird populations. The approach uses a mixture of analyses of long term data, the development of mathematical models that describe the system and the design and implementation of experiments that test hypotheses suggested by the model and data analysis. The experiments then lead to modifications and development of the model and more detailed analysis of long term data.

We think that this approach is crucial if species are to be managed in an effective manner, be it for a sustainable harvest or for conservation reasons. The non-linearities and complexities of ecological systems are such that we feel it is impossible to develop our understanding of even simple ecological communities without using these different but complementary approaches. Our studies on Red Grouse strongly imply that the relative importance of predators and parasites can change significantly over quite short time scales and over comparatively short distances. This suggests that it may be dangerous to extrapolate from the limited studies available for most species and generalise about the overall importance of a particular threat to population viability. In the long run, there will be no substitute for replicated studies on a species carried out at a range of different locations.

Summary

Our long term population studies of Red Grouse have concentrated on the relative importance of different natural enemies throughout the geographic range of this subspecies. The parasitic nematode *Trichostrongylus tenuis* reduces the survival and breeding production of Red Grouse and these effects are sufficient to generate long-term cycles in grouse abundance. Predator populations on moorlands, especially red foxes in Scotland, have increased over the past 30 years. Parasites tend to cause morbidity and increase the vulnerability of grouse to predators. Mathematical models demonstrate that the removal of heavily infected grouse individuals by a small number of predators may allow the size of the red grouse population to increase because the predators effectively reduce the regulatory role of the parasites. However, moderate and high levels of predation result in suppression of the Red Grouse population through predation.

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Hazel Grouse in the Bohemian Forest - results of a 20-year study

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Introduction

Except for the Alps, the Bohemian Forest is the largest area occupied by Hazel Grouse *Bonasa bonasia* in central Europe. I estimate that the population was 2000-4000 pairs in 1993. Before 1950, the density of this species was low, but later an increase was observed, apparently due to habitat changes on extensive areas. After World War 2, thousands of landowners left this region, and forest succession began on abandoned fields and meadows. In addition to the natural regeneration of birch *Betula pendula* and alder *Alnus glutinosa* in all suitable habitats, spruce *Picea abies* was planted, mostly in small plots forming mosaics with a high density of forest edges throughout the whole region. The increase in the amount of young mixed forests was accompanied by a pronounced increase in Hazel Grouse numbers on both sides of the border between Bohemia and Bavaria (Kucera 1975, Scherzinger 1976, Klaus 1991).

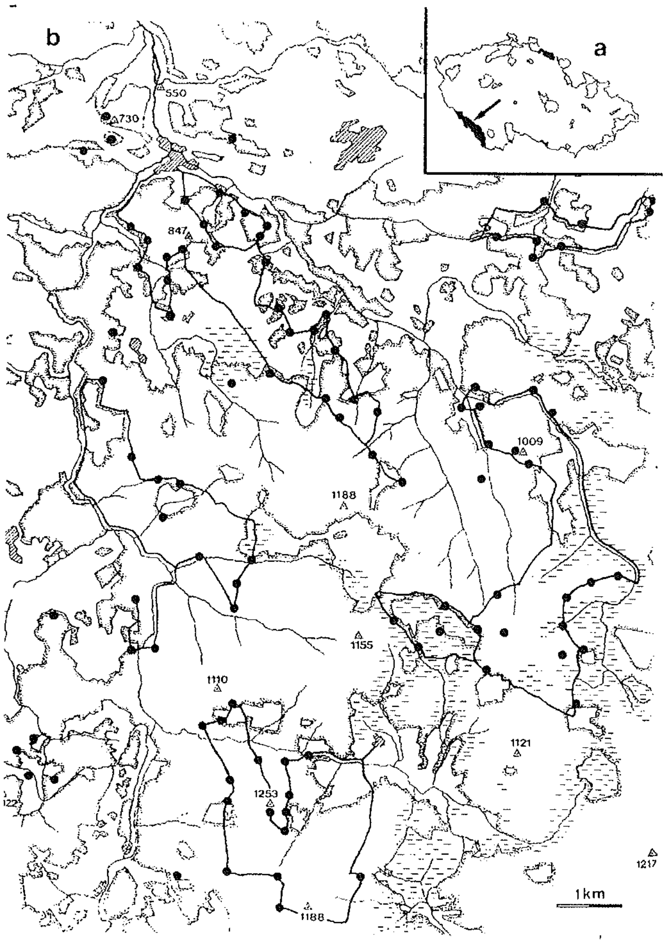

Fig. 1 (a) The location of the study area within the Czech Republic (arrow). Black areas: National Parks, white areas: Landscape Reserves.
(b) Study area in the Bohemian Forest: centres of Hazel Grouse territories (black circles) found along fixed routes (black lines), borders of closed forests (dotted), bogs, hill tops (m ASL) and streams are shown.

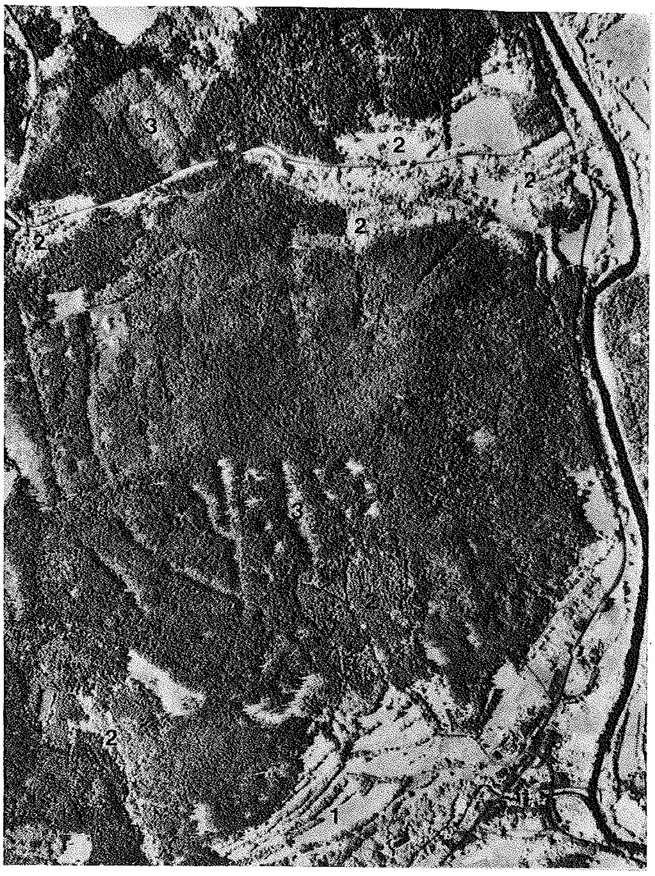

Fig. 2. Aerial photo (taken in June 1990) of the north-western corner of the study area showing extended hedge systems (1), forest succession on abandoned fields (2) and small - scale clearcutting in the older forests (3) - three characteristic features favourable to Hazel Grouse in the study area (by permission from the Czech Institute of Nature Conservation Prague).

In this study, I asked the following questions:

1. Have Hazel Grouse declined during the last 20 years ?
2. Were fluctuations in numbers correlated with weather variables ?
3. How did frequencies of occupation of territories by Hazel Grouse depend on deciduous tree species used for foraging in winter ?

Some results (dependence of Hazel Grouse on tree species diversity and age of the forests) were described earlier (Klaus 1991). A more complex habitat analysis using Swenson's (1991a) method is in progress.

Study area and methods

From 1972-1992, a Hazel Grouse sub-population was studied in the central part of the Bohemian Forest (district Klatovy, Czechia, Fig. 1a, Fig. 2). In an area of 100 km^2, 90 Hazel Grouse territories were mapped along fixed routes (in total 80 km, Fig.1b) using indirect indications (dust-bathing places, droppings, feathers and tracks) and by testing the reaction of males to whistling according to the methods described by Wiesner et al. (1977) and Swenson (1991b). This method assumes that all whistling birds were territorial and that the indirect evidence also indicated separate territories. All data of "territories" are indices rather than direct counts. The study area includes four main types of Hazel Grouse habitats depending on the altitude: valleys with alder as the dominating deciduous tree (about 500-700 m ASL), lower slopes with birch and hazel *Corylus avellana* as the dominating potential winter food (about 700-900 m), mountain mixed forests with spruce, beech *Fagus sylvatica* and fir *Abies alba* where beech buds are the main winter food as indicated by qualitative faecal analysis (900-1100 m), and the natural mountain spruce forests where rowan *Sorbus aucuparia* forms the dominating food in winter when the snow cover is deep (above 1100 m, Fig. 3). Hazel Grouse eat primarily buds and catkins of these four species in winter in this area (L. Kucera and A. Kämpfer-Lauenstein pers. comm. and own unpublished observations).

In 1991, the National Park "Sumava" (Bohemian Forest - 68,520 ha) was founded and the study area became part of this reserve. Until this time, the whole area was managed by forestry with varying intensity. The present study is now continued with permission of the administration of the Sumava National Park.

The number of occupied territories was estimated after the breakup of broods in autumn in 1972, 1973, 1975, 1977, 1981, 1984-85, 1987-90 and 1992, before the beginning of the breeding season in spring in 1976, 1979-80, 1982, 1983, and 1986, and before the breakup of broods in late August 1991. The density index of Hazel Grouse territories (proportion of examined territories that were occupied) found each year was compared with weather conditions during the prelaying (March), laying (April,May), incubation (May, June) and chick periods (June, July) because Swenson et al. (1994) reported a correlation between weather in the pre-laying period and Hazel Grouse reproduction in Finland and Poland. Weather variables were obtained from the Czech weather station at Kasperske Hory (740 m) located at the northern border of the study area. I recorded the total precipitation and the mean of the mean daily temperatures for each month. These factors were used as independent variables to explain annual variation in the density indices. Analysis of covariance was used to determine which weather variables and month were best correlated with bird density. Only significant variables ($p < 0.05$) are discussed here.

Results and Discussion

1. Distribution and frequency of occupancy of Hazel Grouse territories

Figure 1 shows the study area in the central part of the Bohemian Forest. Territories are indicated by full circles in Figure 1b. These circles are connected by solid lines representing the fixed routes where the presence of birds was investigated each year. Forest areas between the circular routes were mainly uniform spruce forests where Hazel Grouse were found only rarely. Depending on the distribution of adequate habitats, the Hazel Grouse was distributed patchily in this area, as also was found by Swenson (1991a) at the Grimsö study area in Sweden.

Hazel Grouse territories were occupied most consistently in old, uneven-aged mixed forests over the 20-year period (Table 1). From such stable habitats, Hazel Grouse presumably dispersed into young successional stages of forest which were suitable for Hazel Grouse only for a few decades in each rotation. Territories located in spruce-dominated mountain forests with a very low density of deciduous trees (*Sorbus aucuparia* or *Betula pubescens* near to bogs) were characterized by a lower frequency of occupancy. We assume that the predation risk was higher in habitats where deciduous trees used for foraging in winter were scattered over large distances (Swenson 1991a).

Table 1. Examples of different frequencies of occupancy of selected, individual territories.

Territory no.	occupied[1]	control[2]	index[3]	habitat type , forest structure
1	13	17	0.76	rowan-type: multilayered old mountain spruce forest
2	14	17	0.82	alder- type: multilayered old pine, spruce, alder
3	13	16	0.81	birch-type: multilayered old pine, spruce, birch
4	12	16	0.75	beech-type: beech-fir-spruce forest, multilayered
5	13	15	0.87	alder-type: pine-spruce-forest, multilayered, alder
7	12	14	0.86	birch-type: pine-birch-spruce forest, multilayered
9	14	15	0.93	birch-type: pine-birch-spruce forest, multilayered
10	12	13	0.92	alder-type: pine-spruce forest with alder , multilayered
12	6	14	0.45	rowan-type: mountain spruce forest, few deciduous
13	5	13	0.38	rowan-type: montain spruce forest, few deciduous
15	7	12	0.58	rowan-type: old spruce forest , few deciduous

1) number of years found occupied, 2) number of years examined, 3) quotient occupied/examined

Table 2. Frequency of territory occupancy (in %) of Hazel Grouse in relation to habitat type.

Habitat type	No.of territories	Frequency of occupancy, s.d.	Difference between habitat types (t-value)	Fisher's programme test	
alder	15	79 ± 2	t = 52.18	k = 33	$p < 0.01$
birch	22	64 ± 3	t = 12.04	k = 32	$p < 0.05$
beech	19	59 ± 6	t = 12.00	k = 27	$p < 0.05$
rowan	13	50 ± 5			

Generally, the frequency of occupancy of a given territory seemed to depend on the altitude and thereby on the availability and/or quality of winter food (Fig. 3, Table 2). Rowan trees were distributed at low density in the mountain spruce forests. Beech was much more common in mixture with spruce. Neither beech nor rowan appeared to be preferred winter food trees. In contrast, alder and birch with catkins were preferred by Hazel Grouse in winter. The dominating role of alder as compared with birch has been described by Swenson (1993). For this reason, we assume a rank order of preferrence of winter food trees used by Hazel Grouse. Territories were classified with respect to the dominant deciduous tree species delivering winter food (rowan, beech, birch and alder type). Territories of the alder-type were occupied in 79% of all cases, followed by the birch type (64%), beech type (59%) and the rowan- type (50%, Fig. 3). By using the Fisher-problem-test , we found that the differences among the mean values of the frequency of occupancy of all four habitat types were statistically significant ($p < 0.01$ to $p < 0.05$, Table 2).

2. Population dynamics

Before our studies began, Kucera (1975) collected data on Hazel Grouse numbers in the same area (200 km^2) and found that numbers increased significantly ($p = 0.05$) between 1962 and 1971 (Fig.4). I found a slight decrease in the index of density in both spring (Fig. 5, top) and autumn (Fig. 5, bottom) during my period of study, but neither regression was significant ($p > 0.1$).

Assuming that Hazel Grouse react to the whistle up to a distance of 80 m and that only territorial birds reply (Swenson 1991b), the 80 km route corresponded to a surveyed area of 12.8 km^2. Thus, the density of occupied territories varied between 2.4 and 5.4 per km^2 between 1972 and 1992. This is similar to Hazel Grouse densities reported from the nearby Bavarian National Park (Scherzinger 1976, Kämpfer-Lauenstein 1995) and other mountain regions in Central Europe (Bergmann et al. 1982). For comparison, in three areas on my study area, 2.0, 2.75, and 3.5 km^2 in size, in addition to the route index, all territories were counted by the same methods and similar density values were found: 5.0, 4.4 and 3.7 territories per km^2, respectively (mean of all years).

The fluctuations found in this study were much less than those found in more northern Hazel Grouse habitats like the Lapland Reserve or the Pechora- Illyich Reserve in the Northern Ural Mountains (Semenov-Tyan-Shanskii 1960, Beshkarev et al. in press) or Finland (Rajala 1966). Fluctuations of grouse usually decline as one moves south (Angelstam et al. 1985). I found only a small difference between the mean densities in spring (3.2 territories / km^2) and in autumn (3.7 occupied territories / km^2) . This could result from the location of my counts in the best habitats. Young birds may have a lesser chance to occupy territories in

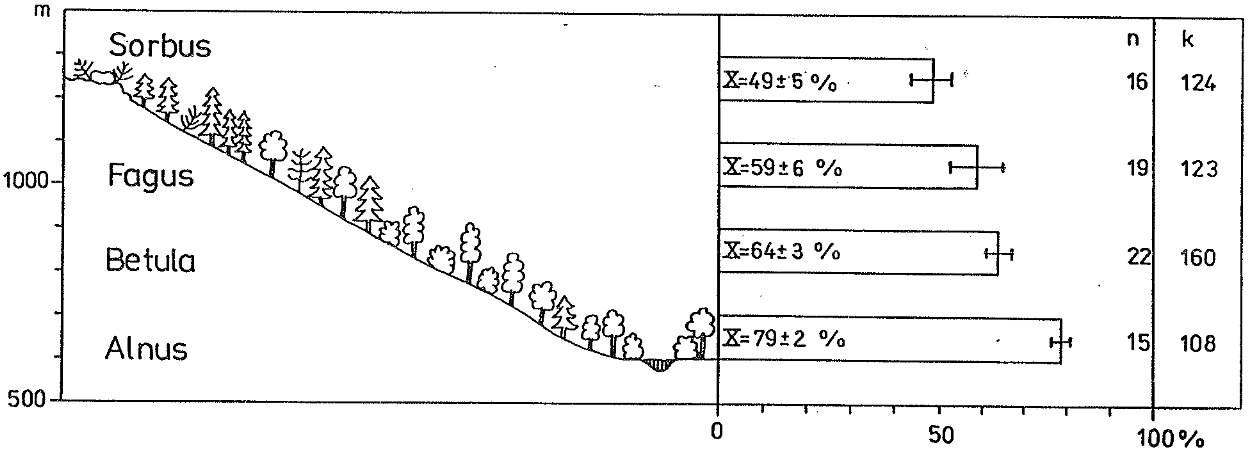

Fig. 3. Frequency of territory occupation by Hazel Grouse in different habitat types (classified with respect to the dominant winter food tree species): n- number of territories found in a given habitat type , k-number of controls (k= n x years). Differences between the means of the occupation frequency are statistically signifcant ($p < 0.01$, Fisher's problem test).

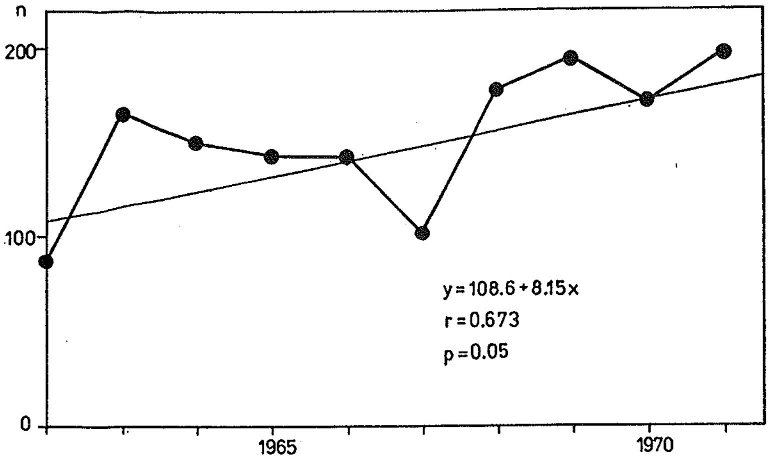

Fig. 4. Number of Hazel Grouse found by Kucera (1975) in his 200 km² study area in 1963-1971.

good habitats and therefore may have been underestimated during my counts. However, the relationship between autumn density and spring weather (see below) does not support this conclusion. Alternatively, there may be small differences between spring and autumn densities in this area, as has been found in Sweden in recent years (J.E. Swenson pers. comm.).

3. Effects of weather on Hazel Grouse density in autumn

Different factors affect the reproductive success of tetraonids, including the physical condition of the female prior to laying (Siivonen 1957, Moss and Watson 1984), weather conditions during incubation (Semenov-Tyan-Shanskii 1960), hatching, or while the chicks are very small (Bump et al. 1947, Slagsvold and Grasaas 1979), and predation on eggs or chicks (Angelstam et al.1985, Marcström et al. 1988).Cold and wet weather increase the mortality of young chicks, which have poorly developed thermo-regulatory abilities (Bump et al. 1947, Slagsfold and Grasaas 1979). Studies showing that reproductive success correlates with weather factors have identified two different periods as most important. These are the pre-laying period and the first weeks after hatching, with small species most affected in the early period, and large species in the latter period (Swenson et al. 1994).

Mean precipitation (1970-1992) at Kasperske Hory (740 m), within the study area, was 55 mm in March, 69 mm in April, 76 mm in May, 104 mm in June, and 110 mm in July. Corresponding average temperatures were 1.6 °C in March, 4.9° C in April, 10.4°C in May, 13.4° C in June, and 15.3°C in July. From these figures, my Bohemian study area was

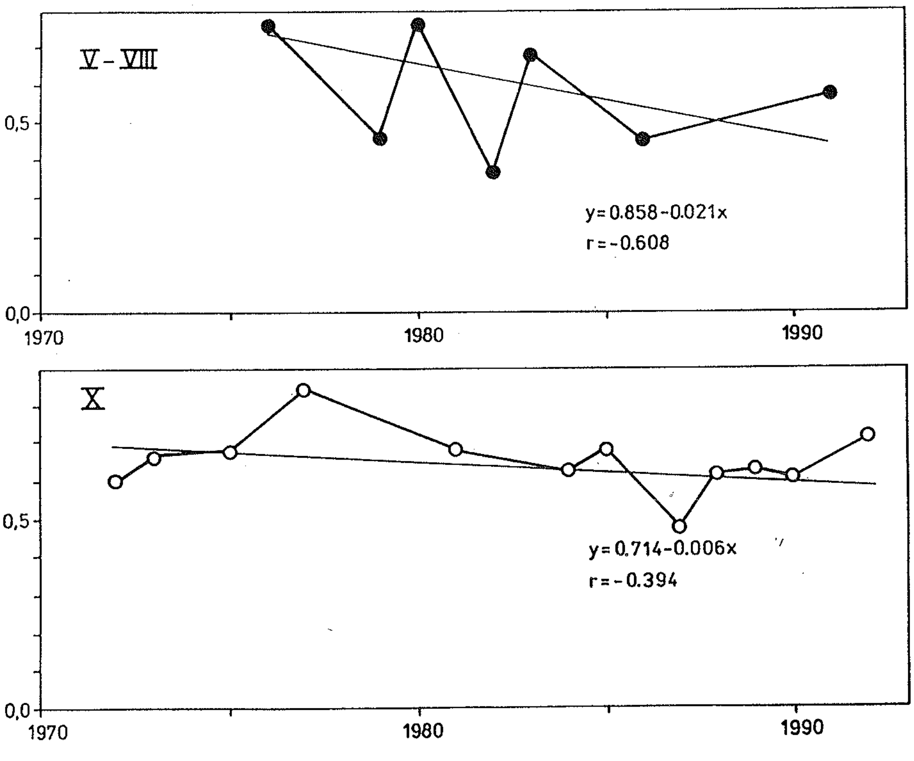

Fig. 5. Index of Hazel Grouse density (occupied territories / examined ones) in spring before the breakup of broods (top) and autumn after their breakup (bottom).

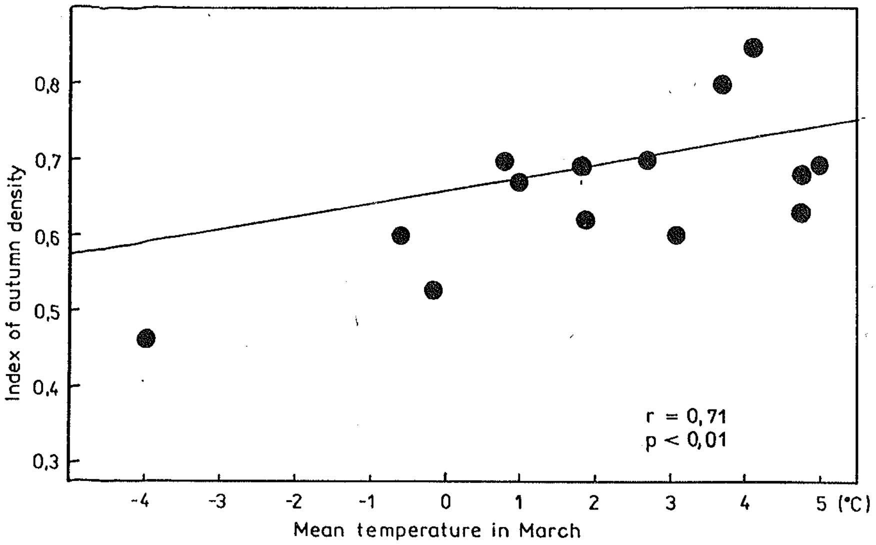

Fig. 6. Relationship between mean temperature in March and the index of autumn density for Hazel Grouse during 20 years in the Bohemian Forest. The index of density was the quotient of occupied territories / examined territories in the given year.

very similar to that described by Swenson et al. (1994) in the Carpathian Mountains and warmer and wetter than the Turku region in southwestern Finland.

I found that the autumn density index was positively correlated ($p < 0.01$) with the mean temperature in March (Fig. 6) as was also reported by Swenson et al. (1994) for two different Hazel Grouse study areas (south-western Finland and southern Poland). These authors argue that the availability of nutritionally rich food and the ability of the females to obtain it during the pre-laying period determines in large part the reproductive success of Hazel Grouse. During this period, female Hazel Grouse forage primarily on newly sprouted forbs (Swenson 1991a). The selection of places with the earliest plant phenology has been documented for other grouse females (Siivonen 1957) and was often observed by us, when Hazel Grouse were found foraging along small streams where ground vegetation was more diverse and became available earliest. Alternatively, March temperatures also could affect adult mortality, which is highest in early spring, especially after a harsh winter (W. Scherzinger pers. comm.). The chance of hens to survive may be enhanced when high quality

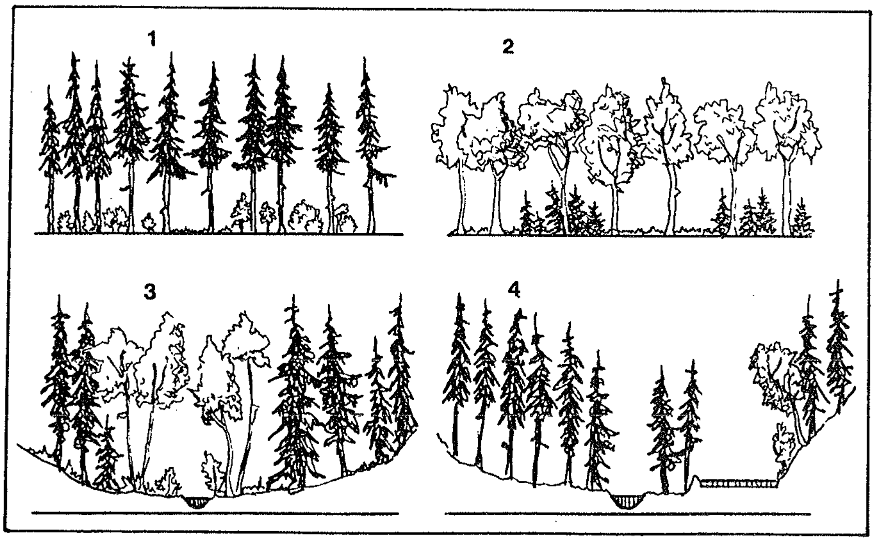

Fig. 7.Possible habitat management for Hazel Grouse: 1- planting of deciduous trees as a second layer in an old, mono-layered spruce forest; 2- planting of conifers as a second layer in a mono-layered deciduous forest; 3- optimal forest structure with alder and spruce close to a stream as a linear connection between habitat patches; 4- undesirable situation: alder is missing, spruce is planted close to the stream bank, the road nearby disturbs Hazel Grouse while foraging in the few deciduous trees left.

food is available early. In my study area, egg laying normally started at the end of April (in the warm spring of 1993 one hen started on 14 April, another hen on 23 April, A. Kämpfer-Lauenstein pers. comm.) and hatching of chicks was observed in the first days of June.

Surprisingly, I did not find a correlation between indices of Hazel Grouse densities in autumn and weather variables after the hatching of chicks (mean temperatures and precipitation in June or July). Eiberle and Matter (1984) compared the number of Hazel Grouse harvested by hunters in Kanton Graubünden, Switzerland from 1919-1961 with temperature and precipitation during bi-monthly periods within and prior to the year of harvest. They found only one significant correlation ($p < 0.05$) with the number of Hazel Grouse harvested. This was the mean temperature during March-April during the year of harvest. Swenson et al. (1994) also failed to find any relationship between precipitation in June or July and reproductive success, in contrast to the situation in grouse with larger body mass such as Capercaillie *Tetrao urogallus*..

Conclusions with respect to species conservation

In this study , a Central European Hazel Grouse population is described. It started to increase after 1950 and has not declined up to the present in a region where commercial forestry has taken place all the time. We can draw some conclusions from this regarding methods of managing forests in order to favour Hazel Grouse in Central European mountain habitats such as the Bavarian Forest, Black Forest, Harz and Oberpfälzer Wald. In general, forestry management to favour Hazel Grouse is not expensive and could be combined with normal forestry, if the following demands are fulfilled (Fig. 7).

- favour deciduous trees including pioneer species (> 10%) in forests dominated by spruce;
- favour spruce and/or fir (> 20%) in pure, deciduous forests;
- favour alder, willow and birch along streams (linear connections linking favourable habitats);
- keep the close vicinity of streams and swamps free from spruce plantations, traffic and forest roads;
- allow forest successions on openings, wind falls, abandoned fields and meadows;
- leave parts of the forest wild including dead trees (standing or fallen)
- promote harvesting of timber in small-scale clearcuts (< 1ha) or as selective or group-felling;
- allow the formation of a second layer (shrubs, regenerating trees) in stands which would otherwise consist only of pole-stage trees;
- favour rich ground vegetation including Ericaceae by reducing high densities of large herbivores;
- control numbers of opportunist predators (corvids, martens, foxes) and wild boar *Sus scrofa* in order to reduce predation on nests and chicks;
- reduce tourist pressure in prime habitats.

Hazel Grouse prefer high species diversity in ground vegetation which is typical of rich soils. Therefore, Hazel Grouse are less sensitive to the input of airborn nitrogen into forest ecosystems than Capercaillie or Black Grouse *Tetrao tetrix*. Both these species are declining or have even become extinct in extensive regions of the Bohemian Forest where the Hazel Grouse population is still stable.

The close proximity of cover and food at the ground and in tops of trees, species diversity in all vegetation layers of a forest , mosaic-like structure of different age classes on a small scale and availability of linear linking structures including streams, hedge systems and forest borders do not help only Hazel Grouse to survive, but also many other threatened species of our forest ecosystems.

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Summary

Since 1972 the distribution, abundance and habitat use of Hazel Grouse *Bonasa bonasia* were studied in a 100 km^2 area of the Bohemian Forest (Czech Republic). Along fixed routes (80 km), all reactions of the grouse to imitations of the male territorial song , as well as indirect indications (dust baths, feathers, droppings, tracks) were recorded. All reactions were assumed to indicate the presence of territorial birds. In the course of the study, Hazel Grouse densities varied between 2.4 and 5.4 territories per km^2. No statistically significant trend in numbers was found. Frequency of occupancy of the territories was highest in rich habitats with alder as a dominant tree (79± 2%), followed by birch (64± 3%), beech (59± 6%), and rowan (50 ± 5%). These trees were presumed to provide winter food. The differences between the frequencies of occupancy of territories located in the four habitat types were statistically significant ($0.01 < p < 0.05$, Fisher's problem test). Territories were patchily distributed in the managed forests. Autumn density was positively correlated with temperatures in the pre-laying period (March).

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Studies of grouse in China

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Introduction

Tetraonidae occurring in China include Capercaillie *Tetrao urogallus*, Black-billed Capercaillie *T. pavirostris*, Black Grouse *T. tetrix*, Willow Ptarmigan *Lagopus lagopus*, Ptarmigan *L. mutus*, Siberian Spruce Grouse *Dendragopus falcipennis*, Hazel Grouse *Bonasa bonasia* and Severtzov's Hazel Grouse *B. sewerzovi* (Fig. 1).

Willow Ptarmigan and Siberian Spruce Grouse

The Willow Ptarmigan and the Siberian Spruce Grouse were not found in investigations in 1984 - 89 in Heilongjiang River valley where they were reported by Cheng Tso-Hsin in 1978. But birds similar to the Willow Ptarmigan are said to have been seen by forestry workers there in November every year.

Ptarmigan

The Ptarmigan is rare and only found in the Altaj Mountains in China. Their habitats include stream sides, forest edge shrubs, meadows and alpine tundra at 1300-3000 m ASL. Foods found in four stomachs were purely herbivorous with some sands, but few studies have been done. The other five species have been studied more in China (Table 1).

Capercaillie

The Capercaillie was first found in the Altaj Mountains area in Xinjiang in 1975 (Chen Fuguan et al. 1980), mainly in coniferous forest at 1500 - 2200 m which is dominated by Siberian epinette *Larix sibirica*, Siberian spruce *Picea obovata*, Siberian pine *Pinus sibirica* and Siberian fir *Abies sibirica*, with few deciduous trees (mainly *Betula* and *Populus* spp.). One lek was found on open ground at the edge of the forest at 1800 m. Breeding biology was studied in 1989 based on six nests, all under fallen trees. Incubating hens did not keep in contact with the males, which were still wandering near the leks. The population density was estimated as 0.23 birds/km^2 with a sex ratio of 1:1.4 (male:female).

Black-billed Capercaillie

The Black-billed Capercaillie is resident in the north of north-eastern China, mainly in the Daxinganling Mountains. Their population and distribution area have been sharply reduced due to increased human disturbance and a big forest fire in 1987. It is now an endangered species in China (Gao Wei et al. 1988). The activities of Black-billed Capercaillie varied seasonally. In winter (November-February), with the lowest temperature -40°C to -50°C, they were inactive and fed mainly on the buds of birches from 1500 - 1600h every day.

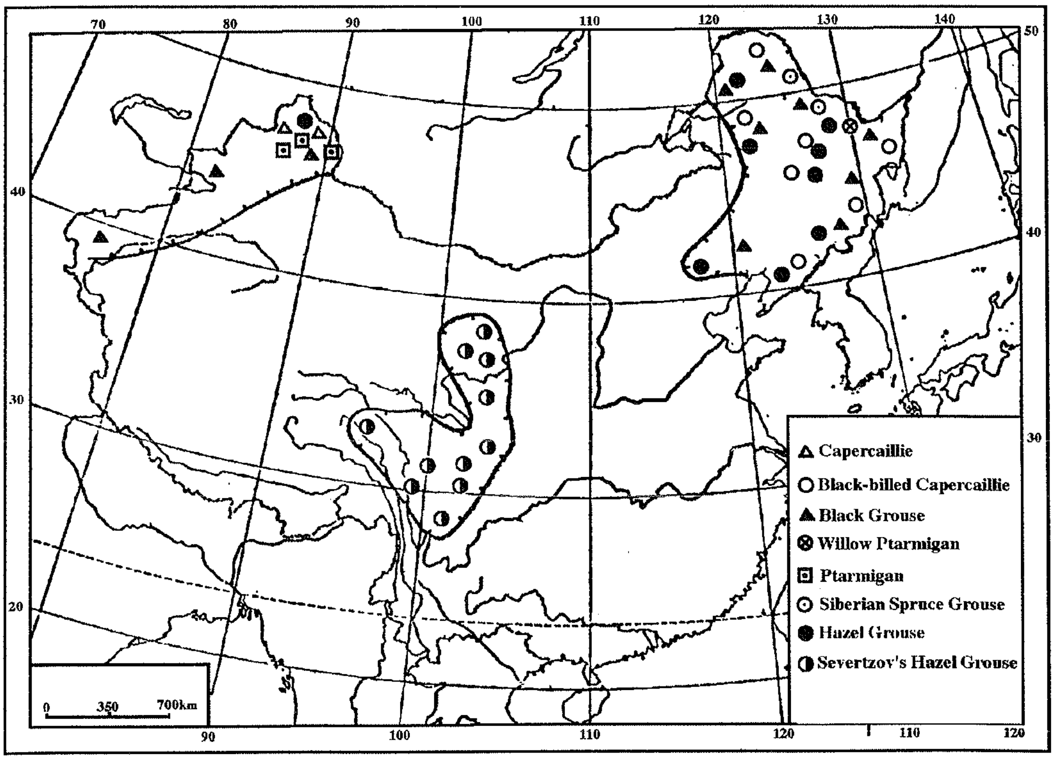

Fig. 1. Distribution of Tetraonidae in China.

Table 1. Studies done on five grouse species in China.

	Tetrao urogallus	*Tetrao pavirostris*	*Tetrao tetrix*	*Bonasa bonasia*	*Bonasa sewerzovi*
Distribution	+	+	+	+	+
Habitat		+	+	+	+
Food composition		+	+	++	+
Food analysis		+	+	++	+
Population density	+	+	+	+	+
Breeding biology	+	+	++	++	+
Chick growth		++		++	
Captive biology		++		++	
Biochemistry			+	+	+
Muscle analysis				+	
Call analysis				+	
Radio telemetry				+	

+: Preliminary studies ++: Well studied

By the electrophoresis analysis of ovalbumin, Black-billed Capercaillie were found to be more closely related to Black Grouse than to Hazel Grouse. This confirmed Mainardi's affinity map of grouse species (Cheng 1978). The ovalbumin consisted of 18 kinds of amino acids, mainly aspartic acid (2.15 x 10^{-6} MOL/ml). Captive studies were done in 1984-87 on artificial breeding and chick growth.

Black Grouse

The Black Grouse occurs from Xinjiang to north-east China, usually at 600 - 900 m, typically in forest and forest-grassland dominated by epinette *Larix* spp., Mongolian Scots pine *Pinus sylvestris var. mongolica*, Asian white birch *Betula platyphylla* and David's poplar *Populus davidiana.* The grassy marshland there provides them with good concealment and nest sites.

The diet of Black Grouse was studied at Buoketu in Daxinganling Mountains from 70 birds (Gao Zhongxin 1975). Vegetable foods were about 89.3%, with animal foods 10.7% in one year, with seasonal variation. In spring, the diet mainly consisted of buds of poplar and willow (70 - 85%); in summer, mainly insects, up to 50% in June; in autumn, mainly fruits of strawberry *Fragaria orientalis*, honeysuckle *Lonicera* spp., bilberry *Vaccinium* spp. and mayberry *Rubus* spp.. From November, their food became buds and twigs of willow and hazel.

The Black Grouse began to breed in late March and early April in north-east China. Leks were found on open ground, extending from 60 to 2900 m^2, depending on the numbers of males displaying. The males displayed both on the ground and in trees. Three nests were found on 10, 12 and 20 May, with clutches of 8, 9 and 10 eggs. All three nests were on the ground in thick grass. The incubation period lasted 26 - 27 days.

Biochemistry studies were done by electrophoresis analysis on ovalbumin. The results indicated that the ovalbumin consisted of 16 kinds of amino acids, mainly glutamic acid (0.132 g/100 ml, 11.7%), aspartic acid (0.118 g/100 ml, 10.4%) and leucine (0.100 g/100 ml, 8.8%).

Populations of Black Grouse have been decreasing. Before 1982, the hunters at Honghuaerji and Genhe in Intermongolia could bag 30 - 50 a day, but in 1985, only 3 - 5 birds. In north Hebei Province in 1990-92, the population density was estimated as 10 - 13 and 6 - 8 birds/km^2 in two sample plots.

Hazel Grouse

The Hazel Grouse is widely distributed and relatively abundant in north-eastern China. It was also found north of Xinjiang recently. They inhabit many different types of forest (Table 2).

Foods eaten by Hazel Grouse were studied (Zhao Zhengjie 1977, Lu Taichun 1991). Results from Xiaoxinganling, Changbai Mountains and Daxinganling were apparently different in different habitats, but all birds

Table 2. Forests in Changbai Mountains, Daxinganling Mountains and Xiaoxinganling Mountains inhabited by Hazel Grouse (all with poplars and birch).

Location	Forest type		
Changbai Mountains	Mixed deciduous/ coniferous	Coniferous	Ermans birch
Daxinganling Mountains	Mixed poplar-birch/larch	Xingan larch	Mongolian Scots pine
Xiaoxinganling Mountains	Mixed deciduous/ coniferous	*Abies* conifer	

were mainly herbivorous, with some insects and small animals, especially in summer. Foods of Hazel Grouse in the bud-feeding period (from early October to late April) were studied in Changbai Mountains from 1983-89 (Yanag Bairan 1993). Mono maple *Acer mono* (21.2%), David's poplar (14.5%), hazel *Corylus mandshurica* (12.2%), Asian white birch (9.5%) and willow *Salix raddeana* (9.4%) were the main foods in this period. These buds were found to contain much protein and high energy materials.

Based on the changes in reproductive organs and compared with body weight, temperature and illumination, Hazel Grouse were thought to come into breeding condition in mid-March to early April (Zhu Zuobin et al. 1988). The clutch size was 6 - 11 (often 8) in Daxinganling and 8 - 12 in Changbai Mountains. Males in Daxinganling were observed to stay near the incubating hens, but males in Changbai Mountains were not observed to have any relationship with the hens after mating on the leks.

Severtzov's Hazel Grouse

The Severtzov's Hazel Grouse is an endemic and rare bird in China, found in Gansu, Qinghai and Sichuan Province. As the result of long-term exploitation of the forest, their northern populations in Qilian Mountain are separated from their southern Qinghai relatives.

The typical habitat of Severtzov's Grouse is in the mountain forest at 2800 - 3200 m, dominated by Qinghai spruce *Picea crassfolia*, Qilian cypress *Sibina przewalskii*, Armand pine *Pinus armandi*, spruce *Picea asperata*, fir *Abies fargesii*, David's poplar *Populus davidiana*, Tianshan birch *Betula tinaschanica* and oak *Quercus liaotungensis*. The climate, especially the temperature, in their habitat is extremely harsh, averaging only 0.9°C with a non-frost period of 115 - 133 days.

Severtzov's grouse were observed to be strictly monogamous, starting pair-formation in early May. Six nests were studied at 2650 - 2800 m in 1983 - 85. Five nests, lined with mosses, feathers and leaves, were located at the base of spruce or fir trees, similar to sites used by Hazel Grouse, but the sixth was different, being found in hollow in a dead spruce tree with a lining of feathers and rotten wood. Five to eight eggs were laid in a clutch, with an average weight of 22.5 g and size 43.8 (43 - 45) x 31.5 (30 - 32.3) mm. Females started to incubate after 2 or 3 eggs were laid. During nest-building and incubation, the males roosted on branches of high trees 30 - 50 m from the nest and when disturbed flew to the ground with flapping wings to warn their mates. The breeding season lasted from mid-May to July, and the incubation period lasted 25 days (Wang Xiangtin et al. 1987).

Food analysis was based on 14 birds from April to December. The main foods were willow and birch buds in winter and early spring, changing to leaves after May. In summer, besides buds and leaves of willows and birches, the birds often fed on flowers, tender leaves of *Berberis* spp., honeysuckle *Lonicera* spp. and *Cotoneaster acutifolius*, and did not miss any chance to capture insects. Their autumn food was mainly on the ground, for example, flowers of *Polygonum* spp., and the tender buds on twigs of *Equisetum arvense*. In late autumn before snow fall, their food was especially the nuts of spruce and *Hippophae rhamnoides*.

Egg protein electrophoresis has been done and compared with the results of Brown Eared-pheasant *Crossoptilon mantchuricum* and Blood Pheasant *Ithaginis cruentus michaelis*. The electrophoresis extinction directive curve of Severtzov's Grouse was similar to that of the Blood Pheasant. Ultra-microscope observation on the egg shells has also been done.

The population density of Severtzov's Grouse was from 0.45 to 1.3 - 2.0 birds/km^2 10 years ago in different areas of Gansu Province. In recent years, numbers have decreased notably except in some natural reserves. Besides predation and parasitism, human activities have been involved. Habitat has been destroyed and unlimited hunting is still very serious.

A hunter in Zhuoni County said that he could kill 60 - 80 grouse every year. It is very urgent to protect this important species effectively and to study it more.

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Seasonal movements by Hazel Grouse in south-central Sweden

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Introduction

The Hazel Grouse *Bonasa bonasia* is generally considered to be sedentary (Gaidar 1973, Bergmann et al. 1982). However, several authors have noted seasonal changes in habitat use and implied that seasonal movements occurred (Ivanter 1962, Gavrin 1969, Kirikov 1975). Pynnönen (1954) even considered the Hazel Grouse to be seasonally migratory. None of these authors gave any estimates of distances that may have been moved. Populations of Spruce Grouse *Dendragapus canadensis* in Canada and Capercaillie *Tetrao urogallus* in Norway were not known to be partially migratory until they were studied using radio-telemetry (Herzog and Keppie 1980, Rolstad 1989). In order to investigate seasonal movements by Hazel Grouse in Sweden, we followed birds marked with radios.

Study area

This was 285 ha, including 195 ha of forest, within a forest reserve on the Grimsö Wildlife Research Area in south-central Sweden (59-60° N, 15-16°E). Most of the forest burned in 1914. The area has received very little forestry management since 1972. It was dominated (56%) by Norway spruce *Picea abies*, birch *Betula pendula* and *B. pubescens* (together 23%), and Scots pine *Pinus sylvestris* (15%). Other deciduous trees (6%) included aspen *Populus tremula*, black alder *Alnus glutinosa*, goat willow *Salix caprea*, and rowan *Sorbus aucuparia*. The reserve was surrounded by intensively managed industrial forests. There, thinning of stands and removal of undergrowth and deciduous vegetation was standard practice. This was unfavourable for Hazel Grouse (Swenson and Angelstam 1993).

Methods

The study lasted from September 1987 to May 1990, and was based on radio-telemetry. Twenty-eight Hazel Grouse were caught in spring and autumn by luring or chasing them into nylon fishing nets. They were fitted with necklace-type transmitters (Kenward 1987) that weighed ≤16 g (4.5% of the birds' weight). Age was determined by the colour of the innermost primary (Stenman and Helminen 1974, Bonczar and Swenson 1992).

Radio-marked Hazel Grouse were located 3-7 times a week. Most locations were based on three bearings, or two if the bird was within 100-150 m. Location accuracy was high, 74% within 20 m of the actual location (Swenson 1993a). All birds were followed until they were killed or until the end of the study; none left the study area undetected.

The year was divided into four seasons: spring (April-May), summer (June-August), autumn (September-October), and winter (November-March). The size and shape of home ranges were measured each season for birds with 25 or more locations using the modified minimum area method of Harvey and Barbour (1965) from a 1:15,000 map with a Kempten planimeter. Overlap was defined as the proportion of the second season's home range that was also within the first season's home range. Overlap was angularly transformed prior to statistical analysis (Sokal and Rohlf 1981). Hazel Grouse were considered to have moved from a home range if there was no overlap between two consecutive seasonal home ranges. The distance between the home ranges of a grouse that moved was the shortest distance from the edge of one range to the edge of the other.

The abundance of seasonally important food plants was determined by surveys of vegetation in summer. Cover of the field vegetation was estimated to the nearest 10% and trees >3 m high were counted on 566 plots, 10 m in radius, located systematically over the entire study area at a density of two per ha. Seasonally important food plants (based on Ahnlund and Helander 1975, Danielsen 1990, Swenson 1991a, 1993b) were: spring, forbs (*Viola* spp., *Anemone nemorosa, Oxalis acetosella*, and *Potentilla erecta*) (primary food) and cottongrass *Eriophorum vaginatum* and *E. anagustifolium* (secondary food); summer, bilberry *Vaccinium myrtillus*; autumn, cowberry *V. vitis-idaea*; winter, black alder (primary food) and birches (secondary food). Bilberry was also relatively important in spring and autumn. Spring and autumn were transitional seasons, with some winter food being consumed at the end of autumn and beginning of spring (Ahnlund and Helander 1975).

Throughout this paper, the means are presented with the standard error of the mean. All tests are two-tailed, and a probability level of 0.05 was considered adequate to reject a null hypothesis.

Results

Sedentary grouse

The radio-marked Hazel Grouse showed a high degree of site fidelity between seasons (Table 1). Of those not moving between seasons, i.e. their seasonal home ranges overlapped to some degree, there was no difference between sexes in degree of home range overlap between seasons (two-factor ANOVA, df=1, F=0.027, p=0.87), but home range overlap from one season to the next varied over the year (two-factor ANOVA, df=3, F=3.30, p=0.03). A one-factor ANOVA revealed that the significant differences in overlap (sexes combined) were between autumn-winter and winter-spring,

Table 1. Overlap of seasonal home ranges of resident radio-marked Hazel Grouse on the study area, and proportion moving to a new home range by season. Overlap is defined as the proportion of the second season's home range that was also within the first season's home range. Movement from a home range occurred when there was no overlap between home ranges in two consecutive seasons.

	Comparisons						
Category and sex	Autumn-winter		Winter-spring		Spring-summer		Summer-autumn
Overlap (%)							
Males	47±7[a](12)		58±10 (10)		42±7 (9)		61±5 (9)
Females	39±8 (8)		78±12 (2)		31±15 (2)		55±5 (6)
Combined	45±5 (17)	*	61±8 (12)	*	40±6 (11)	*	59±4 (15)
Movement from home ranges (N)							
Males	0 (12)[c]		2 (12)		0 (9)		2 (11)
Females	0 (5)		0 (2)		1(3)		1 (7)

[a] Mean±SE (N)
*Significant differences ($p<0.05$)
[c] Number moving (total N)

winter-spring and spring-summer, and between spring-summer and summer-autumn (Fisher protected least significant difference test, $p<0.05$). The mean overlap of winter home ranges during consecutive winters was 47±9% (range of 20-69%, N=4 males and 1 female).

Temporary movements

Relatively few Hazel Grouse moved between seasons, i.e. had no overlap of seasonal home ranges (Table 1). The movements by males in Table 1 were from two adults (≥3 years) whose winter and spring home ranges were separated by 2 and 14 km, respectively; both returned to their previous home range the following September. These movements were not evidence of migration, because both of these males were followed during two years, and both moved only during the year that a female was not present on their home range at the beginning of spring. A third male (8 months old), also without a female, moved 2 km between winter and spring, but was killed before establishing a spring home range. The two movements by females in Table 1 were from one adult (≥3 years) that moved between spring-summer and returned between summer-autumn. This was not a migration either because the edges of the spring home range and summer and autumn home ranges were only 50-150 m apart and the female moved in a summer in which she had chicks, but not in a summer she had no brood.

Permanent movements

During this study, there was only one suggestion of a marked bird moving permanently (not evident in Table 1). A yearling female moved gradually from the spring home range, where it was marked and nested, to a new area for autumn and winter home ranges. The autumn and winter home ranges overlapped each other by 55% and were 600 and 420 m, respectively, from the spring home range. This female was killed by a predator on 1 April, so it was not possible to document if she would have returned to the original spring home range.

Some Hazel Grouse abandoned previous annual home ranges to move on to the study area. Ten Hazel Grouse were captured after acquiring home ranges that had become available after a radio-marked grouse of the same sex died. Of these, five were adults (2 of 4 males and 3 of 6 females) that had presumably held home ranges elsewhere, off the study area.

Spatial relationships of seasonal foods

A correlation matrix of the seasonally important foods (Table 2) showed that the abundance of the most important winter food (alder) was positively associated with that of the most important spring food (forbs). Abundance of the most important summer food (bilberry) was positively associated with that of the most important autumn food (cowberry). However, abundance of spring and winter foods was negatively associated with that of summer and autumn foods.

Discussion

Site fidelity

Hazel Grouse showed a very high degree of site fidelity, staying within a relatively small area throughout the year. Swenson (1991a) reported that seasonal home ranges in this area are relatively small, averaging 15-26 ha. Home range overlap showed that Hazel Grouse used similar areas in winter and spring (61% overlap) and in summer and autumn (59% overlap). Greater shifts in areas used occurred from spring to summer ranges (40% overlap) and from autumn to winter ranges (45% overlap). Thus, our Hazel Grouse used similar areas in winter and spring, then made a shift in their area of use for summer and autumn, and then shifted back to

Table 2. Correlation matrix showing spatial relationships of seasonally important seasonal food plants for Hazel Grouse on the study area, based on their occurrence on 566 plots of 10 m radius.

	Winter foods		Spring foods		Summer	Autumn
	Alder[a]	Birch[b]	Forbs[a]	Cottongrass[b]	Bilberry[c]	Cowberry
Alder	- -					
Birch	+0.146*	- -				
Forbs	+0.216*	+0.081	- -			
Cottongrass	-0.041	+0.200*	-0.067	- -		
Bilberry	-0.160*	-0.165*	-0.205*	-0.155*	- -	
Cowberry	-0.093*	-0.129*	-0.141*	-0.068	+0.282*	- -

[a]Primary food

[b]Secondary food

[c]Bilberry was also often consumed in spring and autumn

*Significant relationship p<0.05

the winter-spring area. However, these were shifts in area, as the seasonal home ranges still overlapped considerably. Our results did not appear to be influenced by the differences in lengths of the seasons, and therefore differing numbers of relocations among the seasons. Winter was 6 months long, summer 3 months, and the other two seasons 2 months. However, home ranges were significantly larger in summer, with no significant differences among the other seasons (Swenson 1991a). Overlap of summer home ranges with those of adjacent seasons was intermediate compared with values from other seasons (Table 1).

The shifts in seasonal use areas were consistent with the distribution of seasonally important foods. The most important winter and spring foods occurred together, as did the most important summer and autumn foods. However, these two groups of foods were significantly segregated from each other on the study area. Our results show that Hazel Grouse habitat contains winter-spring foods and summer-autumn foods within close proximity of each other, i.e. a heterogeneous forest landscape.

There was no evidence of seasonal migration. Two males used spring and summer home ranges that were 2 and 14 km apart, respectively; both returned in September. However, they had not moved the year before, indicating that these movements do not necessarily occur each year. The males appeared to be searching for a mate (Swenson and Boag 1993).

Our results are consistent with the few published data on movements by Hazel Grouse using marked birds. One study, in central-European Russia, was based on ringed birds that were subsequently recaptured (Gaidar 1973). Birds that were ringed as adults moved a median distance of only 150 m (N=27), which was significantly less than the 340 m between sites of capture and death or last location at the end of field work at Grimsö (N=26) (Swenson 1991b). However, Gaidar's (1973) results may have had a bias towards lower distance values because he recaptured birds only within a small study area, thus missing those birds that may have moved beyond its boundaries (Greenwood and Harvey 1982, Swenson 1991b). At any rate, there was no suggestion that Hazel Grouse in Russia moved farther than those at Grimsö. Also, the seasonal home ranges of three radio-marked Hazel Grouse in the Black Forest in Germany all showed some overlap (Lieser and Eisfeld 1991).

Permanent movements

We did find some evidence of Hazel Grouse permanently changing annual home ranges and moving onto the study area. This may have been a movement to better habitat, because the area surrounding the study area was intensively managed forest with less cover near the ground and fewer deciduous trees than the study area. Hazel Grouse densities in the industrial forests averaged about 30% of those in the reserve (Swenson, unpubl. data). Only one marked grouse appeared to change annual home ranges, moving to a new area 420 m away. This bird, a female, was killed on 1 April when almost two years old. The behaviour of other females suggested that she would not have moved from her new spring territory after that date if she had survived (Swenson and Boag 1993).

Management implications

These results are applicable to the conservation of Hazel Grouse. Intensive modern forestry is eliminating or reducing the quality of Hazel Grouse habitats through the loss of cover, draining wet areas, selective removal of deciduous trees, and managing for coniferous monocultures (Danielsen 1991, Swenson and Danielsen 1991). This not only results in less habitat but also fragments the available habitat into smaller and more isolated segments. In a review of the ecological consequences of landscape fragmentation, Opdam

(1990) concluded that site-tenacious species and species with poor dispersal capacities seemed to be the most affected by fragmentation. Our results showed that Hazel Grouse are very site tenacious, and data on juvenile dispersal from Fennoscandia suggest that Hazel Grouse may have a relatively poor dispersal capability, because they showed a median dispersal distance of only 800 m (Swenson 1991b). Based on these conclusions, habitat management that ensures dispersal among the available habitat patches should be the key to the survival of Hazel Grouse populations in fragment landscapes (Opdam 1990).

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Summary

Seasonal movements of Hazel Grouse *Bonasa bonasia* were studied in Sweden using radio-telemetry. Home ranges in adjoining seasons overlapped in 90% of 61 cases. Overlap averaged 45% from autumn to winter, 61% from winter to spring, 40% from spring to summer, and 59% from summer to autumn. The Hazel Grouse used one area in winter and spring, then used adjacent areas in summer and autumn and then returned. These spatial shifts probably reflected differences in distribution of seasonal foods. There was no evidence of seasonal migration, but some birds permanently changed home ranges.

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Distribution and behaviour

Ecological and behavioural constraints on monogamy in the Willow Ptarmigan

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Introduction

In birds, monogamy has been the "neglected" mating system (Mock and Fujioka 1990). Even though over 90% of bird species are monogamous, most studies on avian mating systems have focused on the evolution of polygyny and promiscuity. Monogamy was thought to have evolved because of the need for male parental care (Lack 1968), although recent studies on passerines have shown that this is not always the case (see Bart and Tornes 1989 for review). Monogamy is not common in species with precocial young, presumably because males have been emancipated from parental care. Among the Tetraoninae, however, five of 16 species form pair bonds for at least part of the breeding season (Wittenberger 1978).

Attempts to explain the evolution of monogamy in grouse have focused primarily on the influence of food and predation. Wittenberger (1978) suggested that monogamous grouse species inhabit areas where food is scarce in spring, so that females benefit by associating with males and relying on male vigilance during foraging. He presented no data to support his assertion that food was scarce and this hypothesis has been disputed elsewhere (Bergerud 1988, Hannon and Martin 1992) and will not be considered further here.

Bergerud and Mossop (1984) and later Bergerud (1988) proposed that monogamy developed in arctic and alpine habitats where there were few nest predators, but many avian predators of adults. Here, females did not have to space out their nests to deter predation and were able to live on small pre-laying home ranges that could be defended by males. A pair-bond developed because of the need for males to detect avian predators while females foraged on the territory. Bergerud (1988) stated that ptarmigan have much lower clutch predation rates than species of promiscuous grouse. This, however, is not the case. Willow Ptarmigan *Lagopus lagopus* populations can incur up to 80% nest predation (Myrberget 1985, Martin et al. 1989, Hannon and Martin 1992), White-tailed Ptarmigan *L. leucurus* up to 64% (Braun et al. 1993), Rock Ptarmigan *L. mutus* up to 50% (Weeden 1965), and Hazel Grouse *Bonasa bonasia* are also thought to have high clutch predation (Swenson 1991).

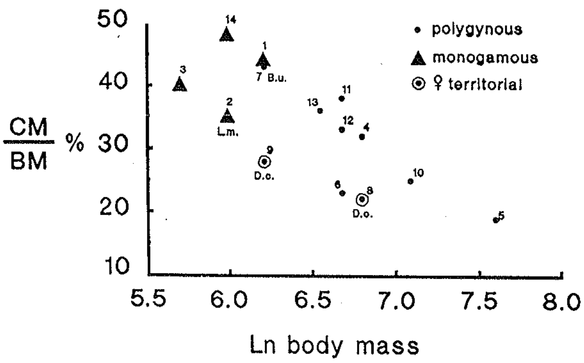

Fig. 1. Clutch mass/body mass ratio plotted against ln body mass for 14 species of grouse. Data on clutch mass and body mass taken from Saether and Andersen (1988); numbers above points indicate species as designated by Saether and Anderson (1988).

Swenson's (1991) hypothesis emphasizes the importance of female body size. He points out that females of monogamous grouse tend to have smaller body size and higher clutch mass/body mass relative to other grouse. He infers that small females are thus under high energy stress so that they need higher quality food and relatively longer foraging time than females of promiscuous species. This leads to female defence of resources and, because of high predation risk, a reliance on male vigilance. The relationship of clutch mass/body size does not hold for all species, however (Fig. 1.). Ruffed Grouse *B. umbellus*, for example, have a high clutch mass to body mass ratio, similar to that of Willow Ptarmigan, yet they do not pair monogamously and in fact may not be territorial. Female Spruce Grouse *Dendragapus canadensis* and Blue Grouse *D. obscurus* have relatively low clutch mass/body mass ratios, yet they appear to defend territories (Stirling 1968, Herzog and Boag 1978, Hannon et al. 1982). Within habitat types (open vs forested), however, females of monogamous species are smaller than females of promiscuous species (Swenson 1991).

In this paper, I review 14 years of study on the monogamous Willow Ptarmigan that my co-workers and I have conducted in the Chilkat Pass area of north-western British Columbia, Canada. I use the cost/benefit approach taken by Wittenberger and Tilson (1980) to test four hypotheses about the evolution and maintenance of monogamy and then present a general explanation for the evolution of monogamy in grouse. The four hypotheses are that monogamy is maintained in Willow Ptarmigan populations because:

1.Females that share male vigilance or parental care (i.e. those paired with polygynous males) have lower reproductive success and/or survival than those that pair monogamously;

2.Males that are polygynous have lower reproductive success (including a lower confidence of paternity) and/or survival than males that pair monogamously;

3.Willow Ptarmigan habitat has a low environmental potential for polygyny (sensu Emlen and Oring 1977); and

4.Males have difficulty attracting more than one female because of shortages of females (both absolute and temporal shortages).

In this paper, I use the term "monogamy" to refer to "apparent monogamy" (Gowaty 1983). This means that birds appear to be paired monogamously but actual mating patterns may not be monogamous if extra-pair copulations are occurring.

Willow Ptarmigan in the Chilkat Pass population are predominantly monogamous (5-20% polygyny occurs annually (Hannon and Martin 1992)). Males accompany their mates from pairing in late April/early May until the end of incubation in early July (Martin 1984) and both males and females defend the brood. During the pre-hatch period, males are more conspicuous than females (Bergerud and Mossop 1984) and give alarm calls for predators (Hannon and Martin 1992). Presumably they are providing vigilance for foraging females against predators.

Study area and Methods

The study area was described in detail by Weeden (1960), Hannon (1984) and Mossop (1988) and general capture and marking techniques by Hannon (1983). Overall, the approach has been to remove monogamous territorial males in spring, creating polygyny (Hannon 1984, Hannon and Martin 1992). The potential costs to males and females were then measured by comparing reproductive success and survival between polygynous and monogamous birds. Radio-telemetry has been used since 1985 (Schieck 1988) to find nests and broods, and time budget analyses were conducted on females from 1986-1988 (Hannon and Martin 1992) and on males from 1988-1989 (Dobush unpublished data). Paternity analysis on chicks was conducted using DNA fingerprinting from 1987-1989 and 1992 (Freeland 1993).

Costs of polygyny to females

Territorial males were removed during two periods in the population cycle. These were at the peak of the cycle and the beginning of the decline (Hannon 1984), and at the low of the cycle (Hannon and Martin 1992). Males responded to the removal of their neighbours by expanding their territories and becoming polygynous. Polygynous males divided their time between their females, so that each female was alone for part of each day. Despite this, overall, the time budgets of females of polygynous males were similar to those of monogamous females (Hannon and Martin 1992). This was because females that shared a mate compensated by feeding more when the male was with them than when they were alone. Females that shared males showed more aggression and other potentially energetically expensive or risky behaviours than monogamous females (Hannon and Martin 1992). Nonetheless, monogamous females and females that shared mates had similar clutch sizes, dates of laying first eggs, similar numbers of fledged young and similar numbers of young recruited the next year (Hannon 1984, Hannon and Martin 1992). There were no differences in nest predation rates, rates of re-nesting or of mortality of females within the breeding season (Hannon and Martin 1992). Martin and Cooke (1987) found similar results in their removal study of Willow Ptarmigan at low density at La Perouse Bay, Manitoba. Miller and Watson (1978), however, reported that one of the two females in nine bigamous groups of Red grouse *L.l. scoticus* failed to produce young. Pedersen (1993) also found lower survival for "widowed" female Willow Ptarmigan in Norway. I concluded that male vigilance or parental assistance was not necessary for female reproductive success and survival in most years. There may, however, be some years with adverse conditions in which females that share male vigilance or raise young alone have higher mortality than monogmous hens. If these "crunch" years are not predictable, then hens may "prefer" monogamy and this may explain the attempts of hens to repel potential secondary females from their territories.

Costs of polygyny to males

Wittenberger and Tilson (1980) proposed that monogamy may exist in some species because polygyny is costly to males. Polygynous male Willow Ptarmigan usually produced more young than monogamous males (Hannon 1984) and in years of high nest predation usually had at least one female that successfully produced a clutch (Table 1). Return rates of banded males to the study area after winter were similar for monogamous and polygynous males, suggesting that mortality rates were the same (Miller and Watson 1978, Hannon 1984). There may be costs to males of being polygynous, however. Polygynous males had larger territories than monogamous males (Hannon 1984). Thus, costs of territorial defence and mate guarding of two or more females may have been higher than those for monogamous males. In addition, Martin and Hannon (1988) reported incidents of attempted extra-pair copulation in Willow Ptarmigan, suggesting that polygynous males may suffer a higher risk of kleptogamy.

Dobush (unpublished data) examined potential costs to males. She observed polygynous and monogamous males prior to the laying period and found that polygynous males spent more time in vigilance behaviour, fed less, and flew

Table 1. Proportions of polygynous and monogamous males that produced a brood in three years of varying nest predation in the Chilkat Pass, northwestern British Columbia.

Year	Nest predation (%)	Polygynous	Monogamous	p
1986	20	83% N=12	95% N=81	0.22
1987	71	68% N=19	33% N=48	0.009
1988	45	90% N=19	62% N=45	0.02

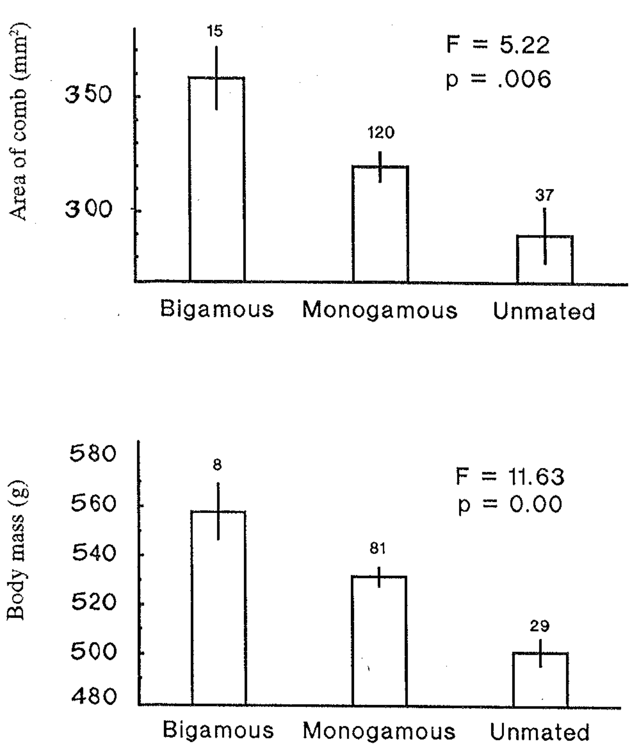

Fig. 2. Body mass (g) and comb area (mm²) for polygynous, monogamous, and unmated male Willow Ptarmigan. Sample size above bars; vertical lines are SE.

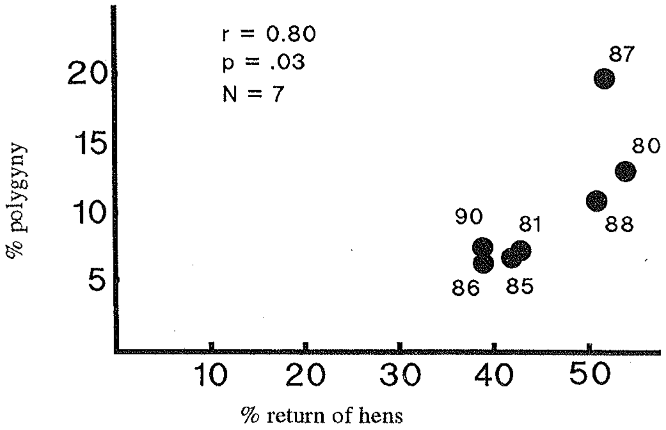

Fig. 3. Percentage of male Willow Ptarmigan that were polygynous in year x+1 plotted against percentage of females banded in year x that returned to the study area in year x+1.

more than monogamous males. Although polygynous and monogamous males had similar numbers of male intruders on their territories, significantly more of these intrusions resulted in disputes with polygynous males and more of the intruders on polygynous males' territories were observed to associate with a female. Consistent with this, Freeland (1993) found that polygynous males suffered higher kleptogamy than monogamous males: 37.5% of 8 broods of polygynous males had extra-pair paternity compared with 7.4% of 27 broods of monogamous males.

Males that become polygynous naturally were not a random sample of the population. Polygynous males tended to be older (86% of polygynous males (N=51), compared with 64% of monogamous males, were more than one year old (N=348)). Polygynous males also had a higher body mass and larger combs than monogamous males (Fig. 2). Perhaps only the "best" males were able to defend larger than average territories and were able to cope with potentially larger energetic costs associated with polygyny.

Low environmental potential for polygyny

Emlen and Oring (1977), in a modification of Orians' (1969) polygyny threshold hypothesis, proposed that some species may be monogamous because there is a low environmental potential for polygyny (EPP). This may be because of low variability in the quality of territories. Although territory quality was not measured directly, indirect evidence indicates that territory quality in the Chilkat Pass may have low variability. Schieck and Hannon (1989) compared the order of settling of two sets of yearling females onto the territories of males in early spring. Territories of males were plotted, females with previous breeding experience were removed, and the settlement patterns of yearling females were monitored. These yearling females were then removed and the settlement patterns of a second set of yearling females was observed. We predicted that if some territories or males were better than others, then the order of female settlement should be similar for the two sets of females. In fact, there was no correlation between the order of female settlement in the two phases of settlement. In addition, there was no relationship between date of settlement of females and vegetation characteristics of territories or characteristics of males (Schieck and Hannon 1989). The only consistent relationships were that females did not settle on small territories and that only males with large territories became polygynous. Habitat quality (as measured by breeding density) in the Chilkat Pass is probably quite high compared to other areas where Willow Ptarmigan breed. Thus, the EPP hypothesis should be tested over a wider range of habitats before it can be rejected.

Constraints on males of obtaining multiple mates

Monogamy may be rare in Willow Ptarmigan because of constraints on males of obtaining more than one mate. Three factors which may limit the availability of females are high breeding synchrony, shortages of females due to higher female mortality, and female-female aggression. Ptarmigan breed in arctic and alpine environments where breeding seasons are short. All first nests were initiated within an 11-day period in the Chilkat Pass (Hannon et al. 1988). This restricted the amount of time that males had to attract additional females. Females were aggressive to females in spring prior to laying (Hannon 1983, Martin et al. 1990). By the time the primary female began incubation, it was too late in the season for the male to attract a second female. Thus, only males with territories large enough to encompass the territories of more than one female could become polygynous. Overall, females had lower survival than males (between 1980 and 1989, annual survival of males was 56.4% (N=529) and for females was 45.8% (N=631); G=30.8; p<0.01). Thus, shortages of females may develop. When female overwinter survival was high, the proportion of males that became polygynous was high as well (Fig. 3).

Evolution of monogamy in grouse

Although the explanations for the evolution of monogamy in grouse have varied (Wittenberger 1978, Bergerud and Mossop 1984, Swenson 1991), two elements, food and predation, were emphasized. In my view, these are indeed the main factors that have led to the evolution of monogamy in some grouse species. The first prerequisite for the evolution of monogamy is the economic defensibility of food resources by females. That food of monogamous species is defendable is supported by the fact that females of all monogamous grouse species have been reported to be aggressive or territorial in spring (Watson and Jenkins 1964, MacDonald 1970, Hannon 1983, 1984, Martin et al. 1990, Swenson 1991). However, no systematic study has compared the quality and distribution of grouse foods across species that have different mating systems.

The second prerequisite to the evolution of monogamy is that the territories of males and females must overlap. There are several promiscuous species of grouse in which females appear to be territorial (e.g. Blue Grouse, Spruce Grouse) but territories of males and females do not overlap. Territories should overlap when females that associate with males do better than females that do not. Pair bonds may be favoured in response to predation risk in open habitats (arctic, alpine or moorland), or in species that are particularly vulnerable to predation (Hazel Grouse), or in species that have short breeding seasons that must maximize their opportunities for foraging (ptarmigan and Hazel Grouse). Our ability to measure costs to females of foraging without males may be limited if females can compensate behaviourally (as in my study) or are able to accumulate costs to the non-breeding season. For example, females that share mates may spend less time foraging, but this may not be expressed in reduced clutch size or chick mass if body reserves are depleted to maximize reproduction, at the expense of over-winter survival. In my removal experiments, promiscuity was never produced, and thus I could not measure costs of no male assistance to females.

The third factor that may lead to monogamy in grouse is the cost of a polygynous pair bond. Polygyny was costly to females in some years (Hannon and Martin 1992) and due to kleptogamy was costly to some males (Freeland 1993). In general, there did not seem to be a high environmental potential for polygyny in Willow Ptarmigan due to demographic constraints (shortages of females), low variability in territory quality, and aggression by females preventing males from attracting additional hens. Thus only the largest and oldest males were able to become polygynous. More experimental studies are required on other species of monogamous grouse to test whether these three factors apply more generally.

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Summary

Members of the genus *Lagopus* are among the few species of grouse that are monogamous. Here I report on research conducted over the past 14 years to understand the ecological and behavioural factors that have led to the development of monogamy in the Willow Ptarmigan. Experiments involving removal of males, done at the peak and low of the population cycle, indicated that females do not usually suffer from having to share a male with another female, but in some years females that shared mates survived less well over the winter. Polygynous males had similar survival rates to monogamous males but produced more fledged chicks than monogamous males. However, DNA fingerprinting revealed that polygynous males had a higher probability of raising young that were fathered by another male. Males that were naturally polygynous were older, had a higher body mass, and had larger territories than monogamous males, suggesting that only the "best" males were able to become polygynous. Only a few males were able to become polygynous in any year and over the long-term this probability was affected by the number of available females and the ability of territorial females to deter the settlement of potential secondary females on territories. Variation in territory quality (apart from size) appeared to be relatively low, suggesting that there was a low environmental potential for polygyny. I discuss the relevance of my findings for Willow Ptarmigan to other species of monogamous grouse.

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Spatial distribution and habitat preference of male Capercaillie in the Pechora-Illych Nature Reserve in 1991-92

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Introduction

The preference of Capercaillie *Tetrao urogallus* for seral stages of the boreal coniferous forest has long been common knowledge among hunters and naturalists (Semenov-Tian-Shansky 1960, Seikskari 1962), but only recently has the dynamic nature of seasonal habitat preference, territorial behaviour and bird density been documented through the use of radiotelemetry (Wegge and Rolstad 1986, Wegge and Larsen 1987, Rolstad and Wegge 1987a, Rolstad et al. 1988). These studies have shown that Capercaillie males in spring occur in sub-populations around local lek sites. In suitable habitats these leks are regularly spaced, with approximately 2 km between lek centres. The birds make distinct movements to seasonal habitats from the leks.

Most recent work on habitat use and spatial distribution of Capercaillie in the northern boreal forest has been done in Scandinavia, particularly in Norway. Scandinavian forests have been altered and fragmented by industrial forestry for more than a century. As they also represent the westernmost limit of the continental distribution of the Capercaillie, it is not known whether the findings from the Scandinavian studies apply generally within the large northern range of the bird.

Here we report a study of Capercaillie in the undisturbed forests of the Pechora-Illych Nature Reserve of northern Russia. We investigate seasonal habitat preference and movements of male Capercaillie radio-collared at one of the largest leks of the reserve. We also compare locations of leks with spatial distribution of forest types within the reserve. Results are compared to those reported from Scandinavian studies of Capercaillie.

Study area

The study area was a 15,800 ha section of the Pechora-Illych Reserve in the north-eastern corner of European Russia (62°N, 57°E). The reserve section and uncut adjacent forest covers approximately 20,000 ha and occurs as an island surrounded by logged forests (Beshkarev et al. 1995). The area is typically flat, northern Russian taiga dominated by pine *Pinus silvestris* (Table 1). Spruce *Picea abies* occurs in narrow bands along streams and fens. Bogs and small meadows along the banks of the Pechora River cover about 9.0% of the reserve.

Methods

During the springs of 1991 and 1992, 17 male Capercaillie (11 adults and 6 two-year olds) were fitted with radio-collars. They were tracked until spring 1993. A bird's position was determined by triangulation, using a hand-held antenna and a compass. Compass bearings were taken at a minimum of three positions from a distance of 50-200 m. Only triangulations with a longest side less than 50 m (precision level ± 25 m) were accepted. Birds were located daily for two separate 7-day periods within each of three time-intervals: 15 February - 2 April (winter), 15 April - 6 June (spring), 13 June - 10 July (early summer). In addition, the birds were located during one week in early August (late summer) and one week in mid October (autumn). Due to transmitter failure and predation, the number of radio-collared birds decreased over the year with 17 in the spring, 16 in early and late summer, nine in autumn, and seven in

Table 1. Proportion (%) of trees of various age classes within the study area of the Pechora-Illych Nature Reserve.

	Age class of trees in years					
Species	0-20	21-40	41-80	81-160	161-300	Average age (yrs)
Pinus silvestris		12.0	18.6	12.4	34.7	140
Picea abies		0.1	0.2	1.1	8.8	158
Abies sibirica and *Pinus sembra*				0.2	0.02	184
Larix sibirica		0.1				30
Betula sp.	0.01	0.01	2.0	0.1	0.2	49
Total	0.01	12.21	20.8	13.8	43.62	

winter. The number of bird positions for each period was 238 in the spring, 224 in the early summer, 112 in late summer, 63 in autumn, and 98 in winter. Occupancy centres for each bird and period were defined as the intersection of the average distance of locations measured along the x and y coordinates from the lek centre. Birds were aged according to beak measurements using the method of Moss et al. (1979) as modified by Wegge and Larsen (1987). The study area was defined as the area containing 95% of all bird positions.

Four forest types identified and mapped in the reserve by the Russian forest survey were used as units of habitat classification: 1) wet pine forest, with abundant growth of Labrador tea *Ledum palustre*, 2) pine/bilberry *Vaccinium myrtillus* forest, drier pine forest without Labrador tea, 3) dry pine forest, with cowberry *Vaccinium vitis-idaea*, and lichens, 4) spruce forest, where spruce comprised more than 50 % of the timber volume (dominating the riparian forest along rivers and creeks but also occurring on upland sites as scattered stands within wet pine forest and pine/bilberry forest). Pine bog, *Sphagnum* bog with scattered pine trees, covered less than 1 % of the study area and was not included in the habitat study.

Within each forest type, forest structure and important food plants for Capercaillie were recorded on $(50\ m^2)$ circular plots. Ten plots were located in each forest type. We recorded density of understory (number of trees/ha), average height of understory, proportion of spruce in understory, horizontal cover of ground vegetation extending more than 40 cm above ground, and horizontal coverage of food plants, *Vaccinium* spp. and herbs.

Preference for forest types was determined as proportion of bird locations within one forest type compared to the area proportion of this habitat in the whole study area.

To investigate the relationship between location of leks and forest composition, we covered the forest map of the reserve with 2x2 km squares and determined the proportion of the five forest types and occurrence of leks within each square.

The index of preference for forest types was calculated according to the method of Ivlev (Ivlev 1961) and we used the chi-square and Bonferroni z test (Neu et al. 1974) to determine level of significance. We used the Student t-test for the analysis of forest characteristics and distance between occupancy centres and spruce forest.

Results

Forest type analyses

Due to large standard deviations, few of the parameters used to describe forest structure and occurrence of food plants were statistically different between forest types. Tree species composition and occurrence of important forage plants are given in Table 2. There were more herbs in the spruce forest than in the other forest types ($p < 0.0001$) and more bilberry in the pine/bilberry forest than in the the dry pine and spruce forests ($p < 0.0001$). Of the parameters used to describe forest structure, wet pine forest had a higher coverage of field vegetation above 40 cm (mainly Labrador tea) and dry pine forest had significantly less spruce in the understory and a lower horizontal cover of forage plants than the other forest types ($p < 0.05$). The other measurements of forest structure did not differ significantly ($p > 0.05$) between forest types.

Table 2. Tree species composition (A), important forage plants (B) and horizontal coverage of field layer >0.4m (C) within the four[1] forest types of the Pechora-Illych Nature Reserve in 1991-92.

Forest characteristics	Forest type				
	Wet pine	Pine/bilberry	Dry pine	Spruce	
				Upland	Riparian
A. Tree composition, stem volume %[2]					
Pinus silvestris	52	65	92		7
Picea abies	13	16	0		68
Abies sibirica	0	1	0		14
Pinus cembra	1	1	0		6
Betula sp.	34	17	8		5
B. Forage plants, horizontal coverage %[3,4]					
Vaccinium myrtillus	11(10)	39(23)	8(5)	6 (4)	4 (7)
Vaccinium oxycoccus	6 (3)	0	0	0	0
Andromeda polifolia	7 (7)	0	0	1 (1)	0
Herbs and ferns	6 (6)	8 (5)	0	36(16)	63(31)
C. Horizontal coverage of field layer %>0.4m[3,4]	37(15)	15(12)	9(5)		13(11)

[1] Pine bog not included

[2] No data on upland spruce forest

[3] Average ground coverage within 50 m² plots

[4] Standard deviation in parenthesis

Bird dispersion and movements

For the year as a whole, 95% of bird locations were within a square of 9 km^2 (3.2 x 2.8 km) (Fig. 1). In spring, the radio-collared males had their occupancy centres within 1 km of the display ground ($\bar{x}$ = 510 m). During this period, males were solitary and did not associate with each other, but we were not able to determine whether they maintained exclusive, non-overlapping home-ranges. Four males stayed close to the lek throughout the year. For the others there was a movement of occupancy centres away from the lek during early summer. Seven moved about 1.6 km to the south and their summer home ranges did not overlap with those used during the lek season. The average distance travelled from the lek to summer occupancy centres for all birds was 1.2 km, with 2.4 km being the longest movement.

Fig. 1. Seasonal occupancy centres of male Capercaillie in the Pechora-Illych Nature Reserve in 1991-92. Location of study area, see Fig. 2

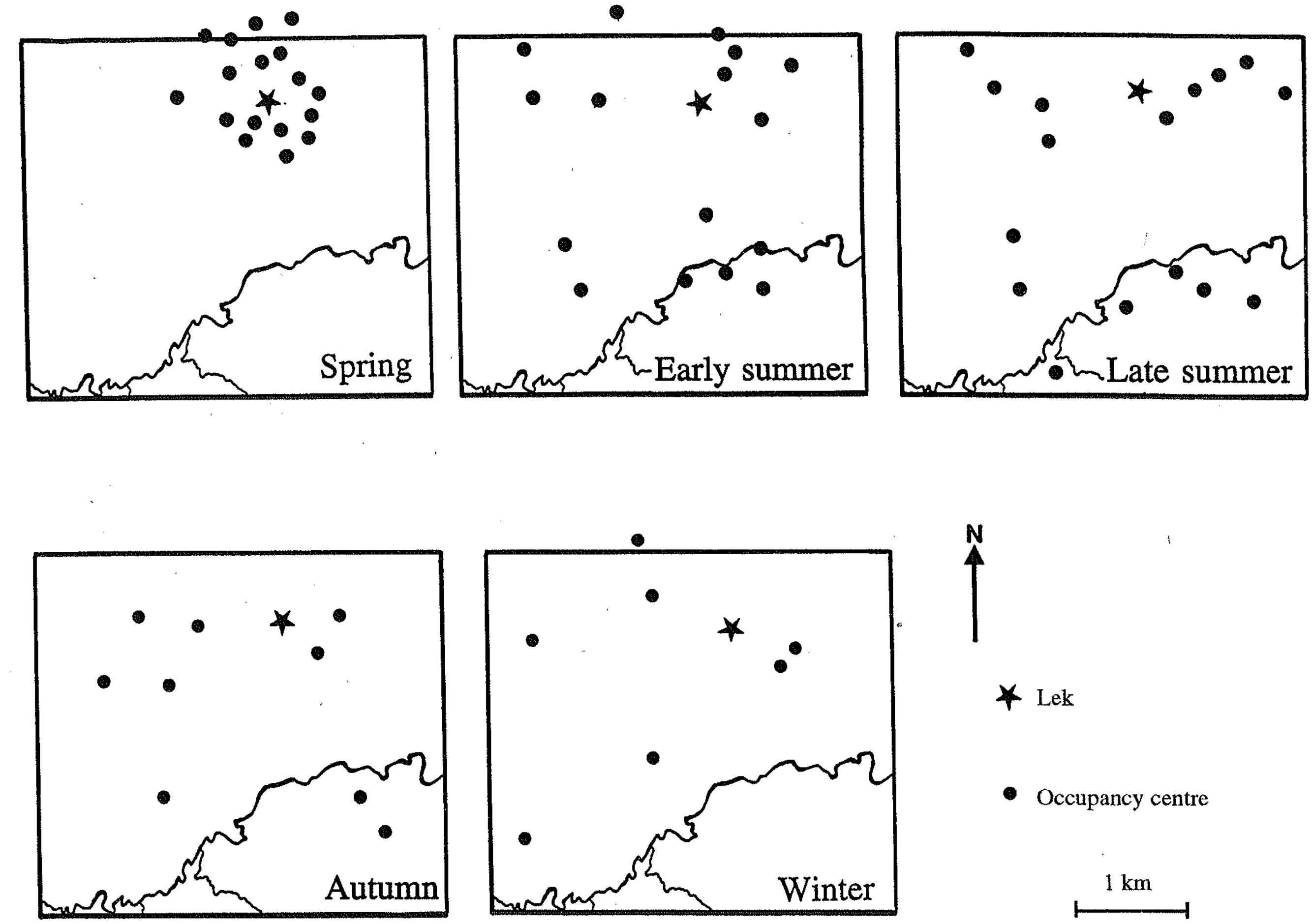

Table 3. Preference (positive index)/avoidance (negative index) of radio-collared Capercaillie males for forest types within the study area in the Pechora-Illych Nature Reserve in 1991-92, in relation to availability of forest types within the study area.

	Forest type, index of preference[1]			
Season	Wet pine	Pine/bilberry	Dry pine[2]	Spruce
Winter	0.09	-0.15	-0.81**	0.20*
Spring	-0.06	-0.06	-0.46*	0.34*
Early summer	0.12	-0.07	-0.58**	0.13
Late summer	0.14	-0.13	-0.21	-0.04
Autumn	0.09	0.03	-0.52**	0.34*
Availability within the study area %	28	33	19	17

[1] Ivlev's (1961) index of preference

[2] Difference between use and availability according to Bonferroni z-test

*p<0.05, **p<0.01

Table 4. Difference in forest composition on 2x2 km^2 squares with and without Capercaillie leks in Pechora-Illych Nature Reserve in 1991-92.

Forest type	Coverage within squares (%) With lek	 Without lek[1]
Wet pine	24	9
Pine-bilberry	36	23
Dry pine	19	53*
Spruce	16	5*

[1] Significant difference between squares with and without leks according to Student's t-test *p<0.05

From August to October, five of nine birds moved their occupancy centres back closer to the lek. Two of these and two birds that remained in outlying home ranges survived to February/March, but there was no further change in location of activity centres over the winter. We did not detect any difference between adults and two-year-olds in seasonal movement and dispersion except for one two-year-old that moved to another lek as a three-year-old (the year after it was radio-collared).

Habitat preference

When off the lek in spring, birds generally stayed in clumps of spruce within the open pine forest surrounding the lek (Table 3). Feeding was in pine intermixed with spruce trees.

In early and late summer, birds showed no significant preference for any one forest type (Table 3). However, the distance from occupancy centres to edge of riparian spruce forest was generally less than 100 m and significantly shorter than between random points and the edge of this forest type within the study area ($p<0.001$)(Fig. 1). When disturbed in the pine forest in summer, birds would almost invariably walk to the spruce forest where, if flushed, they would be hidden by a dense understory.

In autumn (October), the birds started to feed in pine trees and by winter (February-March) pine was the sole forage. From autumn on, they again preferred spruce-dominated forest. In winter, this was mainly clumps of upland spruce within the pine forest (Table 3). In autumn, they started moving away from the riparian spruce forest, although remaining closer than expected from random locations ($p<0.05$). The seven birds that survived to late winter showed no affinity for the riparian spruce forest ($p>0.05$).

Leks in relation to forest composition

There were 19 leks within the reserve, or 1.2 leks per 10 km^2 (Fig. 2). The least distance between leks was c. 2 km, but many leks were isolated from neighbouring leks by more than this distance (Fig. 2). When 2 x 2 km squares with and without leks were compared, there was significantly more spruce forest and less dry pine forest in squares with leks than in squares without leks ($p< 0.05$) (Table 4). Also, there were more wet pine forest and fewer swamps in squares with leks but this was not statistically significant.

In squares with leks, there were generally continuous spruce, wet pine and pine/bilberry forests, while bogs and dry pine forest occurred as islands. In squares without leks, dry pine forest or bogs tended to cover most of the area with the other forest types as islands.

Discussion

Our work confirms that male Capercaillie undertake distinct seasonal movements (Wegge and Rolstad 1986, Rolstad et al. 1988, Rolstad 1988). They stayed within 1 km of the lek during spring but at the end of the display season most birds moved to separate summer habitats. In October, there was another period of habitat shift, when some birds moved back closer to the lek. Similar autumn movements have been reported from Norway (Rolstad et al. 1988). The birds we studied did not undertake longer migrations, by-passing several leks and suitable habitats as do some Norwegian Capercaillie males (which travelled up to 10 km) (Rolstad et al. 1988). The average distance between activity centres of spring and summer was slightly shorter in our study area (1.2 km) than reported from Norway (1.5 km) and considerably shorter than reported from Finland (2.2 km) (Rolstad et al. 1988, Helle et al. 1990). A possible explanation for this difference may be that fragmentation of Scandinavian forests due to modern forestry may force Capercaillie to search a wider area for suitable habitats.

In the mixed coniferous forest of northern Europe, spruce forest rich in herbs and bilberry appears to be an important constituent of Capercaillie summer habitat (Semenov-Tian-Shansky 1960, Rajala 1966, Rolstad et al. 1988, Helle et al. 1990). The birds we studied moved towards the riparian

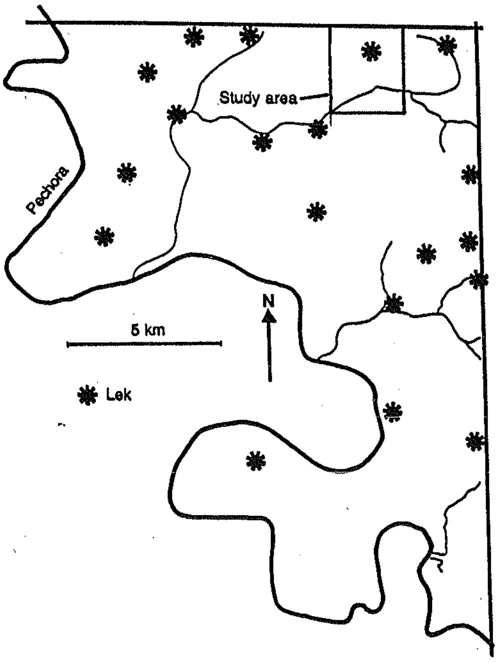

Fig. 2. Distribution of Capercaillie leks in the Pechora-Illych Nature Reserve in 1991-92.

spruce forest that surrounded the lek at distances from 0.3 to 2.0 km, but none went beyond this zone. These narrow corridors therefore formed the boundary of the year-round range of the birds.

There are few extensive studies of food preference of adult Capercaillie in summer but the diet appears to be varied, consisting of leaves, twigs and berries of Vaccinium species and bog rosemary *Andromeda polifolia* besides herbs and ferns from eutrophic growth sites (Semenov-Tian-Shansky 1960). Berries increased in importance towards autumn (Semenov-Tian-Shansky 1960). The search for a varied diet may be the reason why the birds did not prefer any one forest type in our study area during summer. Although Capercaillie males moved from pine forest towards spruce forest in June, Rolstad et al. (1988) concluded that they used vegetation types within their home range in proportion to availability, except for pine bogs, which were avoided.

Use of forest types during summer probably reflects a need for cover, as well as a search for food. The higher usage of wet pine forest compared to pine/bilberry forest during summer (although not significant) may be due to better ground cover in the wet pine forest (Table 2). The ground movement of birds to spruce forest before taking wing and flying away may be a protection against avian predators, particularly the Golden Eagle *Aquila chrysaëtos*. The Golden Eagle is an important predator on Capercaillie in the area, but is not well adapted for hunting in dense forest (Pechora-Illych Research Station, unpublished material).

In autumn, winter and spring, there was a significant preference for spruce- dominated forest, mainly clumps of upland spruce within the pine forest. Such preference for mixed pine/spruce forest has also been demonstrated in Norway (Gjerde 1991). Because pine is the staple food of Capercaillie in winter and spring and an important part of the diet in the autumn (Semenov-Tian-Shansky 1960), spruce probably reflects the need for protection against predators and low temperatures (Gjerde 1991) and possibily against harassment from other males during spring (Wegge and Rolstad 1986).

The wet pine forest and the pine/bilberry forest both contained stands where pine dominated and spruce was intermixed (13-16 % of volume, Table 2). Such stands were used by the Capercaillie, but because they contained less than 50% spruce, they were recorded as pine forest on our maps of forest types and therefore also in our data set. Therefore our study is likely to underestimate Capercaillie preference for mixed pine/spruce forest. One of the reasons why male Capercaillies avoided dry pine forests may be that these forests lacked spruce.

Compared to male Capercaillie of the Pechora-Illych reserve, Scandinavian birds show a higher preference for spruce forest during summer, particularly towards late summer (Rajala 1966, Rolstad and Wegge 1987b, Rolstad et al. 1988). This difference is probably explained by the abundance of bilberry in Scandinavian spruce forests. In our study area, bilberry occurred in pine forest, particularly in pine/bilberry forest, while herbs predominated in the spruce forest (Table 2.) The tendency to higher usage of pine/bilberry forest towards late summer may reflect a search for ripening bilberry by the birds which we studied (Table 3).

The difference in forest composition in squares with and without leks supports the findings from the habitat preference study. There was 2-3 times more dry pine forest and only a third of the spruce forest in squares without leks compared to those with leks. Large areas of continuous dry pine forest appear to be inferior habitat for Capercaillie and to have low densities of birds. Although the Capercaillie showed preference for spruce within forests dominated by pine in this study, Capercaillie density decreased in forests to the east of our study area where spruce was the dominant tree (Beshkarev et al. 1994). Optimal male Capercaillie habitat of the northern Russian taiga therefore appears to be pine forest with abundant spruce.

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Summary

Seasonal movements and habitat preferences of Capercaillie in northern Russian taiga forest were investigated using 17 radio-collared males. Birds jointly used 9 km^2 as their year-round habitat. In spring, they stayed within 1 km of the display ground. In June, seven of 16 birds made distinct movements towards riparian spruce forest, averaging 1.2 km from the lek site. Some of the birds moved back towards the lek in early autumn. Spruce forest appeared important as cover throughout the year, while dry, lichen-dominated pine forest was avoided. The least distance between leks within the reserve was approximately 2 km, but the leks were more dispersed in areas dominated by continuous dry pine forest.

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Dispersion and habitat selection of displaying male Black Grouse in the Mont Avic Natural Park, western Italian Alps

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Introduction

Studies on Black Grouse *Tetrao tetrix* reproductive behaviour conducted on the Italian side of the Alps have shown differences in habitat selection, frequency of solitary displaying males, and average dimension of leks (Bocca 1987, Celada in press, de Franceschi 1981, 1989, Quaglino and Motta 1988, Scherini et al. 1985). Here I report on habitat selection and solitary display by male Black Grouse observed in the western Italian Alps during the springs of 1986-1993.

Study area

The study area of 1940 ha was located in the valley of the Chalamy stream, a tributary of the Dora Baltea river in the south-east of Aosta Valley (50°60'N, 3°90'E) and mostly within Mont Avic Natural Park. It includes large forests where mountain pine *Pinus uncinata* is dominant, but larch *Larix decidua* and Scots pine *Pinus sylvestris* are also present. Other landscape features include subalpine pastures, peat-bogs, ponds, small lakes and scree slopes. The timberline is dominated by Ericaceae (mostly *Rhododendron ferruginea, Vaccinium myrtillus, V. vitis-idaea, V. gaultherioides*) and by *Juniperus communis*, with grassy spots, rocky outcrops and scattered bushes above the timberline. Habitats suitable for the Black Grouse occur at 1400-2250 m and extend without interruption northward and southward. Nowadays, traditional sylvicultural and pastoral activities occur locally, and the study area is frequented by tourists in summer. Less than 10% of the male Black Grouse seen in spring are killed annually by hunters in autumn. On the whole, human activities do not seem to have much impact on the local population of Black Grouse.

Materials and methods

In 1987, 1991 and 1993, one total count was made each year simultaneously in May at all the display sites on the study area. Display sites were also visited outside the census dates in all years between 1986 and 1993 in April, May or June. During these eight years, each display site was visited a total of 4 to 18 times. In order to define environmental parameters, only locations on which displaying males had been sighted during the first 1.5 hours of the morning singing period were considered display sites. All males which occupied sites at a distance of more 100 m from the nearest other male were considered to be soloists.

The data on hydrography and vegetation used to describe the environment near each display site came from maps prepared by the Mont Avic Natural Park. The surface of the potential area utilized by Black Grouse was calculated according to the method proposed by Ellison et al. (1981). By this method, potential habitats include all areas where grouse are seen at any time of year.

An index of habitat selection was calculated according to the method of Ricci et al. (1990), where:

$$SI = \frac{\text{number of males observed within the habitat type}}{\text{number of males expected, based on the area of the habitat type}}$$

Statistical analysis of the indices was carried out using the method of Byers et al. (1984).

Results and discussion

Habitats potentially suitable for Black Grouse covered 1940 ha. They were a complex mosaic, with only the dense mountain pine forests occurring in large homogeneous blocks.

Counts showed at least 60 displaying males in 1987, 65 in 1991 and 53 in 1993, or a density of 2.7 - 3.4 cocks/100ha. Other data available for the Alps (Bocca 1987, Bordignon and Motta 1991, De Franceschi in Brichetti et al. 1992, Ellison et al. 1981, Magnani and Landry 1981, Marti and Pauli 1983, Meile 1982, Miquet 1984, Picard 1983, Zbinden 1985) suggest that this density is rarely exceeded on areas of more than 500 ha in the Alps, although locally 7-8 males/100 ha can be observed.

Out of the 177 display sites identified (Fig. 1), 31 were known to have been occupied at least four times during the eight years by 1-5 displaying males (13 with one male, 9 with 2, 6 with 3 and 3 with 5). Distances between adjacent display sites which were simultaneously occupied were 100-200 m in 30% of cases, and 100 -500 m in 84% of cases (n=325; Fig. 2). These distances in Mont Avic Park are apparently similar to those reported in various French alpine areas (Ellison et al. 1981). However, in Northern Europe (for instance Koivisto (1965) in Finland, and Johnstone (1969) in Scotland), reported distances between leks were greater.

All display sites were at 1650-2200 m (maximum 2050-2100 m), mostly on north-east slopes, as might be expected from the local geography. Sixty-seven per cent of the display sites were on slopes exceeding 10°, 24% were on ridges or crests, and only 9% on plateaux or hollows with little inclination.

In May, displaying males were watched on 536 sites.

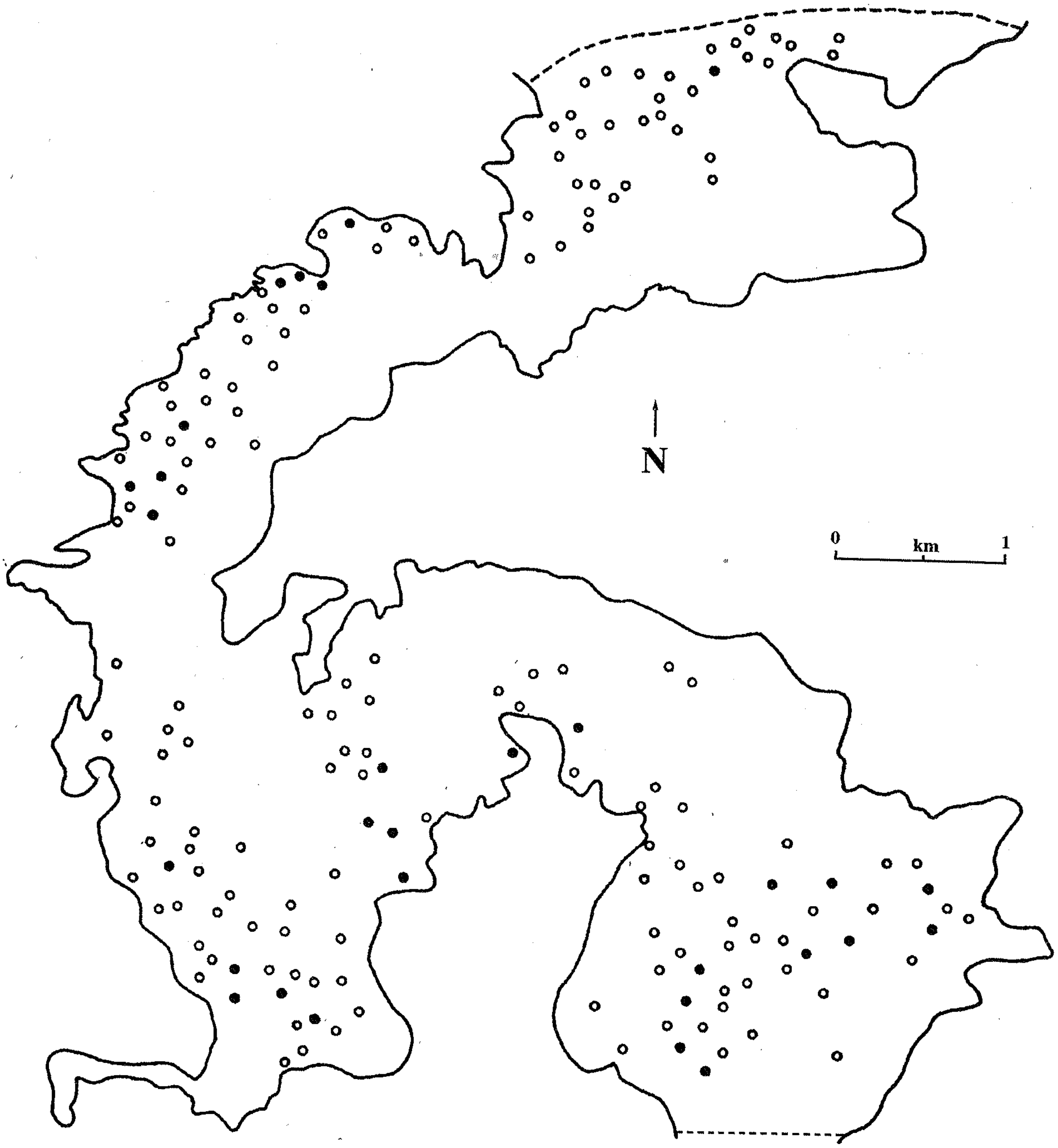

Fig. 1. Location of display sites in 1940 ha in the Chalamy Valley in 1986-93.

o Unstable or temporary display sites

• Regularly occupied display sites (4-16 observations in different years)

One hundred and fifty-five of these sites were totally covered with snow, 269 were partially covered, 142 had only a little snow and 10 had none.

Expected and observed proportions of use of habitat types differed significantly ($X^2 = 478.9$; d.f. = 9; $p = 0.0001$) (Table 1). Open larch woods (SI = 2.66) and scattered shrubs alternating with herbaceous vegetation (SI = 2.36) were significantly selected by displaying males ($p < 0.05$). Scattered shrubs were also preferred in Finland (Koivisto 1965). Subalpine pastures, considered to be optimal in other sectors of the western Alps (Isenmann et al. 1970, Magnani and Landry 1981) were avoided at Mont Avic. Dense mountain pine forests with more than 40% tree canopy were used less than expected. Nevertheless, about 19% of displaying male Black Grouse were in this type of habitat. Displaying in dense forests, even though not usual (Glutz et al. 1973, Klaus et al. 1990), has also been reported by Arndt (in Couturier and Couturier 1980). Areas with shrubs over 60 cm high were avoided. No displaying males were seen on scree slopes next to woods, even when snow completely covered the rocks.

The males seen showed a limited tendency to form stable leks. Of 602 males, soloists accounted for 33-71% (average 53%) of the total population between 1986 and 1993 (Table

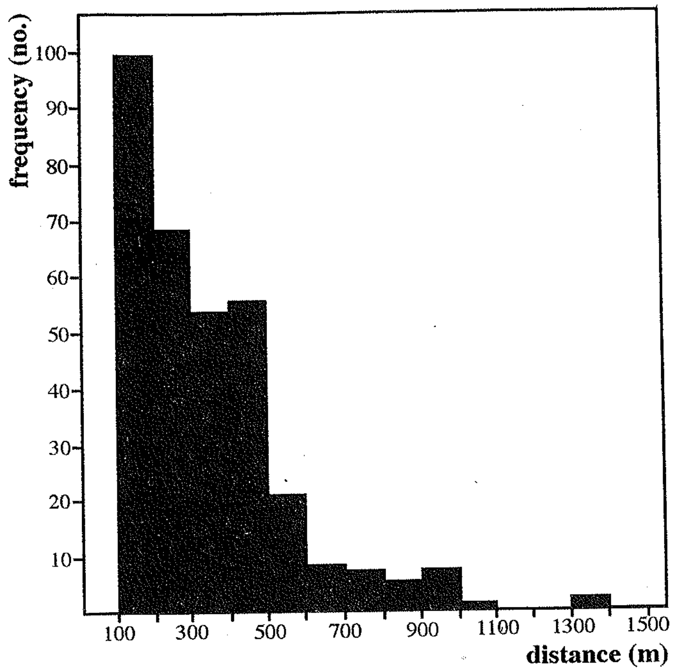

Fig. 2. Distances between adjacent display sites used simultaneously (n = 325).

2). These proportions are high compared to those of other areas (Bocca 1987, De Franceschi 1989, Ellison et al. 1984, Mattedi 1986, Màrti and Pauli 1983, Rotelli and Zbinden 1991, Zbinden 1985). However, in another protected area in the Italian western Alps, Val Troncea Natural Park, all the displaying Black Grouse were solitary (Celada in press). Zbinden (1985) noted that both habitat structure and age of males in a population can influence group size of displaying males. Perhaps the steep irregular terrain on the Mont Avic area does not favour lek formation.

Males may move up to 200 m during the course of their morning display (Bocca 1987, Couturier and Couturier 1980). This was also seen in my study area in cases where mating was recorded. It is therefore possible that "itinerant" display sites are occupied not only by young males, but also by males more than 2 years old. The influence of snow melt on the position of display sites in the Chalamy Valley should be investigated further, although the position of leks did not change much from year to year, as reported by Koivisto (1965) in Finland.

Table 1. Habitat type selection by displaying male Black Grouse observed in the Chalamy Valley, 1986-93.

Habitat types**	Area (ha)	Displaying males Observed no.	Observed %	Expected %	SI*	Bonferroni's interval %	Habitat selected or not
1	333	274	45.5	17.2	2.66	39.9-51.1	selected
2	372	98	16.3	19.2	0.85	12.2-20.4	neutral
3	65	20	3.3	3.3	1.00	1.3- 5.3	neutral
4	725	116	19.3	37.4	0.52	14.9-23.7	avoided
5	108	10	1.7	5.6	0.29	0.3- 3.1	avoided
6	106	78	12.9	5.4	2.36	9.2-16.6	selected
7	61	5	0.8	3.1	0.26	0.0- 1.8	avoided
8	19	1	0.2	1.0	0.17)		
9	25	0	0.0	1.3	0.00)		
10	126	0	0.0	6.5	0.00)		
Total	1940	602	100.0	100.0			

$$* \text{ SI (selection index)} = \frac{\text{no., or \%, of males observed within the habitat type}}{\text{no., or \%, of males expected, based on the area of the habitat type}}$$

SI<1 - rate of selection lower than expected)
SI>1 - rate of selection greater than expected) significant at X = 0.05

** habitat types -

1. Open larch woods (canopy closure < 40%), with undergrowth of *Ericaceae* alternating with herbaceous vegetation.
2. Open mountain pine woods (canopy closure < 40%) on rocky soil with stretches of subalpine moorlands.
3. Dense larch forests (canopy closure ≥ 40%), with undergrowth as 1.
4. Dense mountain pine forests (canopy closure ≥ 40%), with undergrowth as 1.
5. Pastures.
6. Subalpine moorlands alternating with small stretches of herbaceous vegetation.
7. Shrubs with average height exceeding 60 cm.
8. Peat-bogs, ponds, lakes.
9. Dense Scots pine forests (canopy closure ≥ 40%), undergrowth with *Arctostaphylos uva-ursi, Juniperus communis* and herbaceous vegetation.
10. Scree slopes.

Table 2. Group sizes of displaying male Black Grouse in the Chalamy Valley, 1986-93.

Lek group size	Years								Total	
	1986	1987	1988	1989	1990	1991	1992	1993	No.	%
soloists	39	52	30	23	17	41	23	88	313	52
2 males	8	13	8	5	4	4	2	11	55	18
3 males	3	2	3	3	3	1	0	3	18	9
4 males	1	2	3	2	3	2	0	2	15	10
5 males	1	6	2	1	1	1	1	0	13	11
Total males	73	122	77	55	51	65	32	127	602	100

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Summary

This study describes locations of displaying male Black Grouse in spring on a 1940 ha area which included dense mountain pine forests, sparse larch woods and a timberline with rhododendron and several species of *Vaccinium.*

Displaying males were widely dispersed, with a limited tendency to form stable leks. The maximum number of males at any display site was five, with birds tending usually to display solitarily, especially in the dense mountain pine woods. Open larch woods and subalpine moorlands were significantly selected for display. Few displaying birds were recorded in subalpine pastures, which are usually thought to be ideal lek sites. No displaying males were seen on scree slopes next to woods, even when snow completely covered the rocks.

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Home range of male Black Grouse *Tetrao tetrix* from summer to winter in the eastern Alps (Friuli, Italy)

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Introduction

Black Grouse *Tetrao tetrix* are distributed in the Western Palaearctic from Great Britain east to Siberia and China. The species occurs over much of the Alps between 1400 and 2200 m, but some breeding birds are also found at 600-700 m in pre-alpine districts (de Franceschi 1992).

This is the first time in Italy that movements and habitat use have been studied in marked Black Grouse. The aim of the study was to obtain specific information on home range size and relative spacing of four males, caught, marked and radio-tagged in spring on two leks of the Eastern Alps. Their movements were followed from May 1991 to January or March 1992.

Study areas

Male Black Grouse were caught and radio-tracked in two areas of the Carnic Alps and Pre-alps in 1989-1993. These areas were selected because of easy access.

Most information was collected from birds marked in spring and summer at Lanza (Carnic Alps) (46° 34' N, 13° 09' E) on an area of about 400 ha (Table 1). The lek was on the Lanza Plans in the western part of the study area, where vegetation included alpine meadows with a few small ponds, tall thickets of mountain pine *Pinus mugo* and small conifer woods.The higher elevations (1600 -1900 m) of the eastern part were covered by a belt of dense mountain pine, containing large openings with Ericaceae and herbaceous vegetation, as well as small streams descending to the meadows and woods below. At lower altitudes, there were open mixed conifer woods composed of larch *Larix decidua* and spruce *Picea excelsa*, interrupted by frequent natural openings, in which were found bushes of mountain pine, *Vaccinium* spp., *Rhododendron* spp., *Salix* spp. and green alder *Alnus viridis*, interspersed in the herbaceous vegetation.

The study area on Mount Cuàr (Carnic Pre-alps) (46° 19' N, 13° 07' E) included a large belt of grazing land (about 100 ha), surrounded by old coppices and stands of beech *Fagus sylvatica*, interspersed with some small patches of spruce. A wide strip of bushes, mainly green alder, raspberry *Rubus idaeus*, *Salix* spp, and *Juniperus communis*, separated the open beech stands from pastures.

Materials and methods

We captured 16 adult and five yearling Black Grouse males, one adult and one yearling female and two young males (Table 1). Of these 25 birds, one young, one yearling, 11 adult males and one female were equipped with radio tags (Table 1).

In late spring, several (15 to 20) large nets (2 x 20 m each) were laid at the leks, from the centre to the border of the display grounds (up to 300 m). The nets were erected after sundown the night before each morning of trapping. Yearling and adult males were caught on leks. The female and young male were captured in summer, using a single 2 x 20 m net after locating birds with pointing dogs.

The radio-tags used weighed 16 - 24 g (1.2-2% of the mean body weight). All birds captured in the 1989-1992 period were back-tagged, except for one young male that was equipped with a radio-necklace. In spring 1993, only radio-necklaces were used. Range of tags was 2-3 km, and battery life 8-10 months. Birds were monitored using a 4-element directional Yagi-antenna (Mod. Fiordo) and a portable receiver (Mod. M57). Locations were obtained by triangulation from high points, usually once a week by at least two people.

To estimate the spacing and the sizes of home ranges of the four radio-equipped males over several months, we retained locations otained both by triangulation (3 or more fixes) and by cross-bearings (at least 2 fixes) (according to Rolstad et al. 1988). For triangulation locations, if the length of any side of the triangle exceeded 200 m, the data were discarded. Likewise, if the location given by cross-bearings was judged to be more than 200 m from the true location of the bird, the data were rejected. Home ranges were drawn by the minimum convex polygon method (Harvey and Barbour 1965). The area obtained was divided into a grid of squares (1 ha each) and contacts with a radio-equipped male were mapped on a field form.

Results

A - Lanza (Carnic Alps) study area

One hundred and five contacts were obtained for male A (yearling) and 157 for male B (adult). Mean distances between the lek and summer occupancy centres (SOC) were 2000 and 500 m respectively. The home ranges of the two radio-tagged birds partially overlapped (Fig. 1). The distance between the most widely separated contacts of each bird was 3000 m (male A) and 1300 m (male B) respectively (Table 2). In summer and early autumn, they spent most time concentrated in individual areas; they did not contact each other and were often located farther than 1200 m from each other. In late autumn and winter, daily movements were less

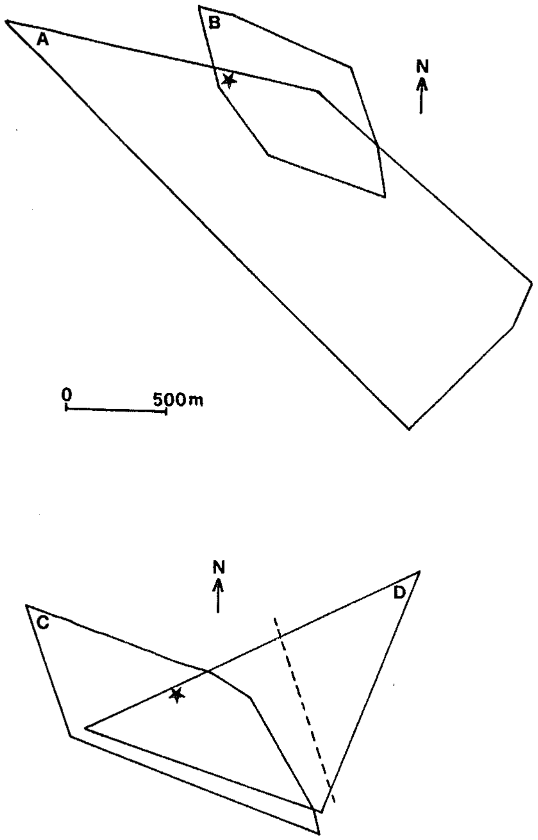

Fig. 1 Home ranges of yearling and adult male Black Grouse in the Carnic Alps (A and B) and in the Carnic Prealps (C and D) (* - Lek). For male D, the area to the right of the dashed line was not included in the calculation of size of home range from June to November (see text).

pronounced than in summer and occasionally both males were found close together. Early in winter, these males flocked with 10 other males which were flushed in the same area. From 3 June 1991 to 2 March 1992, home ranges were 41.5 ha for the adult male and 195.9 ha for the yearling. In summer, male B used mainly small openings in 3 ha of pastures and shrubs interspersed within the mountain pine belt. The high number of contacts in these pastures (73 out of 157) demonstrated the great site tenacity of this bird after display activity had ceased. However, male A changed its range in early summer, shifting from the western to the eastern part of the area and demonstrating a strong site fidelity only in late summer and autumn, using mainly a small area (about 4 ha) in the eastern part of the whole home range. Open larch woods were used mostly in late autumn and winter.

B - Mount Cuàr (Carnic Prealps) study area

Both radio-tagged Black Grouse (C and D) were adult males. Fifty-seven contacts were made with C, and 54 with D. Mean distances between the lek and summer occupancy centres were 550 and 800 m respectively, and between the most widely separated contacts of each male 1850 m (male C) and 1830 m (male D) respectively (Table 2). Throughout the seasons, both radio-tagged birds regularly frequented the shrubby edges of the open beech woods, but separately and not associating with each other. Home range sizes were 66.5 ha (C) and 81.8 ha (D), and they partially overlapped (from 17 May 1991, to 23 January 1992) (Fig. 1).

Male D lost its radio-tag sometime after we last flushed it on 11 November 1991. During late autumn and winter surveys, the contacts with this male (or with its radio-tag) were always in the same direction along a deep creek, difficult to reach. This male may have been killed long before we found its tag (but we do not know when). Excluding the area where the 16 contacts occurred after its last flushing (to the right of the sketched line in Fig. 1), the home range of male D from June to November was c. 48 ha, (other data about this male area given in parenthesis in Table 2).

Discussion

In the eastern Alps, the mean home range size of three adult male Black Grouse from June to January or March was about 66.3 ha, (41.5 for B, 66.5 for C and up to 81.8 ha for D) but pehaps only 51.3 ha if the home range of D was 48 ha (see above). Such mean values are among the smallest recorded in Europe (Table 3). The home range of the yearling (male A) was 195.9 ha, 2.5 - 5 times larger than that of the adults.

Table 1. Numbers of Black Grouse caught at Lanza and Mount Cuàr in 1989-1993. ((*) Radio-tagged birds. Young - birds about 2 months old; yearling - about 11 (or 12) months old in June; adult - about 23 (or 24) months old in June)

Study area	Year	Males			Females		
		Young	yearling	adult	Young	yearling	adult
Lanza							
	1989	1 (*)					
	1990			2			1
	1991		1(*)	1(*)			
	1992	1	2	2 (1)		1 (*)	
	1993		2	8 (2)(*)			
Mount Cuàr							
	1991			2 (*)			
	1992			1			

(1) One male had already been ringed in spring 1990, on the same lek.

(2) One of these males (about 35 months old) had already been ringed as a yearling in spring 1991, on the same lek.

Table 2. Spacing and home range of four radio-tagged Black Grouse. (SOC - Summer occupancy centre.)

Study area	Lanza		Mount Cuàr	
	Male A	Male B	Male C	Male D
No. of tag and age	No.12 (first year)	No. 15 (ad.)	No. 10 (ad.)	No. 14 (ad.)
Observation period	June to March	June to March	June to Jan.	June to Jan.
No. of contacts	105	157	57	54 (38)*
Distance (from the SOC to the lek) (in m)	2000	500	550	800
Distance between most widely separated locations (in m)	3000	1300	1850	1830 (1230)
Home range (in ha)	195.9	41.5	66.5	81.8 (48)

* see text

Table 3. Some home range sizes of adult and yearling Black Grouse males recorded in Europe.

Country	Nos.of birds	Period	Home range (ha)	Reference
Scotland	7	October to June	303-689	Robel 1969a, 1969b
Germany	4	April - May	128-356	Schröder et al.. 1981
Norway	4	Summer	19-43	Rolstad et al. 1985
Belgium	2	Summer	25-70	Klaus et al. 1990
French Alps	4	June to winter	69-234	Houard and Mure 1987
French Alps	11	Autumn	16-312	Ellison et al. 1989
French Alps	8	Winter	4-30	Ellison et al. 1989
Italian Alps	4	June to March	41-195.9	This study

In Norway, a similar relationship was also found between the home range sizes of young and adult Capercaillie *Tetrao urogallus* (Rolstad et al. 1988). In Scotland, a yearling male Black Grouse, caught and radio-tagged on a lek, wandered further in spring (April-May) than adults (Robel 1969b).

In 1989 August-December 1989 at Lanza, the home range of a single radio-tagged young male (60-70 days old) was 31.5 ha, including alpine meadows, mountain pine and alder bushes, and small open thickets of larch (Mattedi, unpublished data).

Recorded home ranges of adult Black Grouse were thus smaller in the Italian Alps than in the French Alps (Houard and Mure 1987, Ellison et al. 1989) (Table 3), perhaps because the three adult males captured on leks at Lanza were territorial and sedentary. Alternatively, such small sizes could be due to the vegetational characteristics providing rich food and shelter throughout both study areas. In the Carnic Alps, the winter home range size (12-27 ha) was as large as in the French Alps (Ellison et al. 1989).

Small sizes of the alpine home ranges may depend not only on the presence close to the leks of pasture lands rich in food and shelter, but also on the reduced size and fragmentation of the suitable habitats, or perhaps on the fact that most males were solitary.

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Summary

Movements of four radio-tagged male Black Grouse were followed from summer 1991 to winter 1991-92 at Lanza (Carnic Alps), and at Mount Cuàr (Carnic Pre-alps). After display activity ceased in June, the males settled at their summer sites, 2000 and 500 m from the lek at Lanza, and 1850 and 1830 m away at Mount Cuàr. Their movements from the centre of their summer ranges, across the slopes of the study areas, averaged 500 m (adult) and 1500 m (yearling) at Lanza, and 800 m (adults) at Mount Cuàr. The home ranges of the three adult males from summer to winter averaged about 51 - 66 ha, being larger in the Prealps than in the Alps. The home range of the yearling was 2.5 to 5 times larger than that of the adults.

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Selection of birch by Black Grouse *Tetrao tetrix* in winter

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Introduction

The Black Grouse *Tetrao tetrix* of the boreal forest has birch *Betula* spp. as its main winter forage (Kaasa 1959, Semenon-Tjan- Shanskij 1960, Pulliainen 1982). Birch dominates the early successional stages of the boreal forest. However, not all birch trees or forest stands may be used by the birds for feeding. A preference for certain trees and tree stands has been demonstrated for Capercaillie *Tetrao urogallus* which select trees rich in protein and low in resins (Spidsø and Korsmo 1994) and which require pine forests of certain densities and spatial heterogeneity during winter (Gjerde 1991a, b). Also, Hazel Grouse *Bonasa bonasia* prefer some alder *Alnus* spp. trees to others (Swenson 1991).

In winter, Scandinavian Black Grouse generally live in forests with a high proportion of birch (Seiskari 1962, Sørensen 1978, Toverud 1981). However, no detailed information exists on the type of birch and forest stands preferred by the birds. In this study, we relate Black Grouse use of birch to age, size, canopy morphology and the catkin production of individual trees. We also studied the effect of birch density and occurrence of Norway spruce *Picea abies* within the habitat. The effect of forestry on Black Grouse winter habitat is discussed and some recommendations for habitat management are proposed.

The forests selected for the study were partly sprayed with a herbicide (glyphosate) to reduce hardwoods in plantations. The project is part of a larger study of the ecological effects of glyphosate application. The study was done in winters 1990-91 and 1991-92.

Study area

The study area of 3.5 km^2 was located in Hurdalen in south Norway. Black Grouse habitat was studied on the valley slopes on the north and south side of the lake Skrukkelisjøen (60°26'N, 10°54'E), from 329 m ASL at the lake shore to c. 600 m at the ridge top. The forest was dominated by Norway spruce which constituted more than 90% of the timber volume. Close to 50% of the forest was younger than 30 years.

Forestry was particularly intensive on the south side of the valley, creating even-aged monocultures of Norway spruce. Here, the plantations have been sprayed with glyphosate to reduce the competition from deciduous brush. Average size of plantations and forest stands was c. 30 ha. The south side of the valley had deep soil of high site quality. On the north side of the valley, forestry was less intensive. On this side, although spruce dominated with scattered pines *Pinus sylvestris*, birch was abundant both intermixed and as pure stands. On the north side, the topography was more rugged and broken with exposed rock outcrops, more variable site quality, and there was little use of herbicides.

The main lek of the study area was on a mire on a small peninsula on the south lake shore. Fifteen-twenty cocks displayed at this lek in each of the two study years. In the winter 1990-91, maximum snow depth was 120 cm while in 1991-92 there were only a few days with 10-20 cm of snow.

Material and methods

Black Grouse use of forest stands was investigated by comparing densities of dropping heaps left by birds roosting in the snow or beneath spruce trees. Heaps which had accumulated over the winter were mapped in May 1991, immediately after snow-melt. The dropping heaps were recorded by two men walking along transects perpendicular to the slope on both sides of lake Skrukkelisjøen. A total of 94 transects with an average length of 350 m was surveyed. In areas with birch, transects were 25 m apart, but in pure spruce forest with low frequency of dropping heaps they were 75 m apart. Only 25% of the pure spruce forest within the study area was surveyed. All heaps of droppings within 2 m of each transect were counted. Numbers and height of tree species taller than 2 m were recorded on circular plots of 4 m radius at 25 m intervals along the transects. A total of 1306 plots was surveyed.

Birch trees used by Black Grouse for feeding in winter were identified during the winter of 1991 by a) the presence of droppings on the snow beneath the trees, and b) by direct observations of birds browsing in the trees. The droppings left by foraging birds occurred singly on the snow surface and were not detectable during the survey of dropping heaps in May. Due to heavy snow in 1990-91, feeding trees were marked and investigation postponed to the winter of 1992. Tree height, diameter, height of the canopy, canopy width and number of catkins were recorded on each tree used for feeding. Diameter was measured 1.3 m above ground and canopy width was defined by a scale from 1 to 4. Young, rapidly growing trees with narrow canopies and thin branches, and old mature trees with wide canopies and thicker branches were given a rating of 1 and 4 respectively. Catkins were counted on 3-4 branches selected at random in the middle of the canopy using binoculars. The number of catkins was averaged per branch. Within a circle of 10 m radius, all trees above 50% of the height of the feeding tree were counted. Each feeding tree was compared to a random (control) birch tree chosen by walking 30 m from the feeding tree on a random compass course and selecting the closest potential feeding tree. Trees less than 50% of the height of the feeding tree were not considered to be potential feeding trees. A total of 114 pairs of feeding/control trees was recorded.

Food choice of Black Grouse during winter was determined from droppings collected in February-March in both winters of the study. In 1991 and 1992, respectively, 70 and 80 heaps of droppings were collected. A composite sample of each dropping heap was disolved in water and 50 random plant fragments were identified and used as an indication of food choice (Blom 1980).

Fourteen male and seven female Black Grouse were captured on the lek and fitted with radio transmitters. During the winter of 1991-92, instrumented Black Grouse were located on average twice in each month.

In the statistical tests, forest composition on each circular plot was compared to the number of dropping heaps along 12.5 m of the transect on both sides of the centre of the plot. Furthermore, the study area was divided, on a subjective basis, into 10 sub-units using density of droppings as a basis. Students t, analysis of variance and linear regression analysis were calculated on Minitab. Paired t, chi-square and Wilcoxon two-sample test were tested on sigma-stat.

Results

Fragments of birch catkins dominated in the droppings of Black Grouse during the two winters of the study (Fig. 1), but the proportion was significantly higher (74%) in winter 1990-91 compared to 1991-92 (47%) ($X^2 = 14.1$, df = 1, $p < 0.001$). In droppings, bilberry *Vaccinium myrtillus* twigs increased from insignificant in 1990-91 to almost 40% in winter 1991-92 ($X^2 = 44.3$, df = 1, $p < 0.001$), while birch twigs decreased from 21% to 6% ($X^2 = 8.4$, df = 1, p = 0.004). Buds were eaten in small amounts and did not differ between the years. We saw no Black Grouse walking on the ground and feeding on birch shrubs.

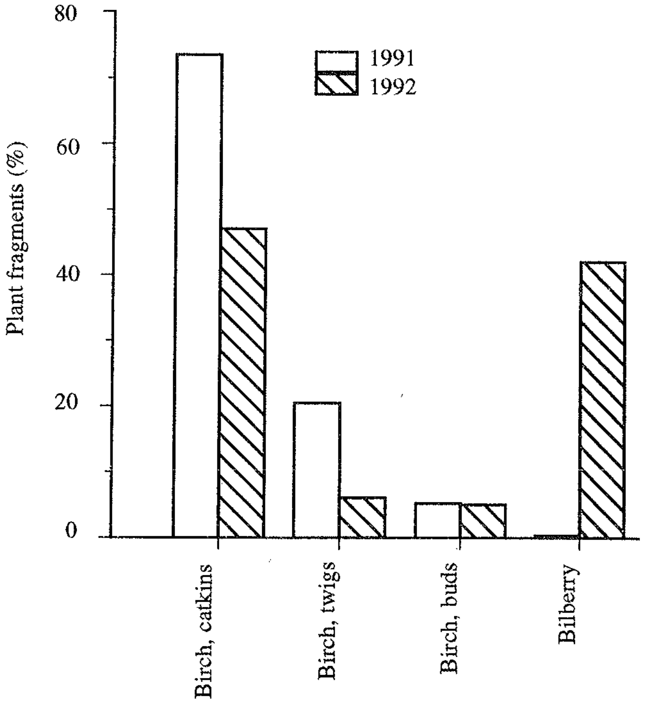

Fig. 1. Fragments of birch and bilberry in droppings of Black Grouse during a winter with normal snow cover (1991) and a winter with sparse snow (1992), south Norway.

Compared to control trees, birch selected by Black Grouse for feeding were taller (paired t = 10.9, df = 113, $p < 0.001$) and had a larger diameter (paired t = 8.9, df = 113, $p < 0.001$). Within stands, feeding trees were almost 33% higher than control trees. Feeding trees also had wider (Wilcoxon signed rank test, N = 114, $p < 0.001$) and longer (paired t = 1.68, df = 113, p = 0.048) canopies and almost twice the number of catkins (paired t = 5.0, df = 113, $p < 0.001$) as control trees (Table 1). Number of catkins, canopy width and stem diameter correlated with height of trees (r = 0.50-0.91, df = 112, $p < 0.01$). Around feeding trees, there were fewer spruce trees (6.7) compared to around control trees (9.9) (paired t = 4.19, df = 113, $p < 0.001$).

There was no correlation between density of birch trees on single plots and density of dropping heaps on 12.5 m of the transect on both sides of the centre of the plots (r = 0.038, df = 1304, p = 0.32). The correlation improved when density of birch trees was compared between the 10 forest stands identified from occurrence of dropping heaps, but the correlation between number of birch trees ha^{-1} and dropping heaps was not statistically significant (r = 0.45, df = 8, p = 0.198). However, when only birch trees higher than 8 m within the 10 stands were used in the analysis, there was a statistically significant increase in density of dropping heaps with increasing density of birch trees (r = 0.66, df = 8, p = 0.041) (Fig. 2). Birch trees used by Black Grouse often had a clumped distribution and occurred in small pure stands with spruce as undergrowth. When single birch trees occurred in old mature spruce forest, few were used for feeding. In the habitats with the highest number of dropping heaps, there were approximately 800 spruce ha^{-1} (25-50 years old), and heaps were frequently found under young spruce with dense branches hanging close to the ground. There was, however, no significant correlation between numbers of spruce and numbers of heaps of droppings along the transects.

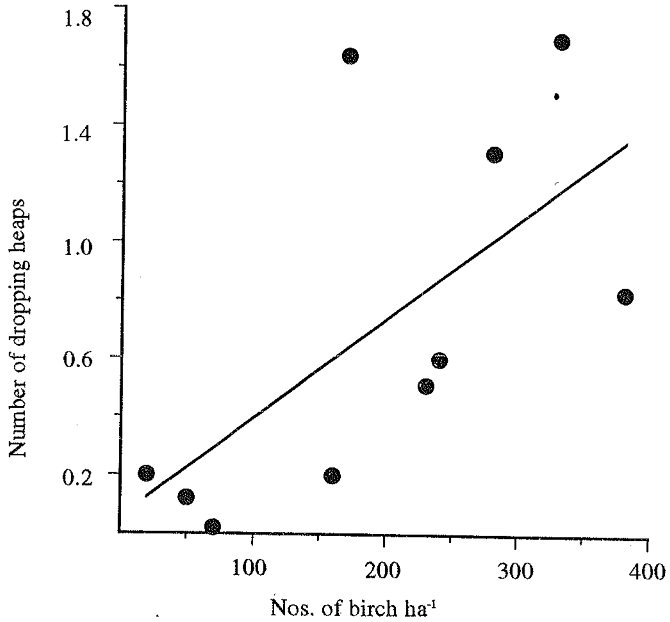

Fig. 2. Number of dropping heaps along 25 m sections of transect lines in relation to density of birch trees higher than 8 m in 1991, south Norway.

Table 1. Height, diameter, canopy width (scale 1-4), % of stem with branches, catkins (average number of male catkins/branch) on birch trees selected by Black Grouse for feeding in winter of 1991 and 1992 in south Norway, compared to control trees.

	Height m	Diameter cm	Canopy width	Proportion of stem with branches %	Catkins
Browsed	14.5±3.9	20.2±9.8	2.8±0.8	60.0±15.2	42.8±35.1
Control	10.9±4.1	12.6±7.3	1.9±0.9	56.9±15.3	22.2±26.5

Snow roosts (burrows) usually occurred on small openings within the forest where the snow had a loose and 'fluffed' structure. Snow beneath birch trees, which had hardened due to snow falling from branches above, was generally not used for roosting.

Birch trees were more abundant on the south-facing slope (265 trees > 8m ha^{-1}) than on the north-facing slope (22 trees > 8m ha^{-1}), and the density of dropping heaps along the transects also differed between the south- (11 ha^{-1}) and north- (2 ha^{-1}) facing slopes ($t = 8.10$, $p < 0.0001$, $df = 1304$).

In winter 1991-92, all radio-locations of instrumented females were on the south-facing slope north of the lake (N = 12). Nearly 90% of instrumented males were also located on this slope (N = 56). The remaining 10 locations of Black Grouse were scattered on the hill slope south of the lake, and in most cases in association with the sparse occurrence of birch.

Discussion

We frequently observed snow burrows used for roosting in birch forest where Black Grouse fed, while few burrows were found in areas devoid of birch (Hjeljord unpubl.). Sørensen (1978) concluded from winter studies of Black Grouse in our study area that roosting in the snow generally occurred within 50 m of feeding trees. This conclusion is supported by other studies where the birds were found to roost close to the feeding sites, often diving into the snow from the feeding tree (Klaus et al. 1990). We therefore believe that the locations of snow burrows give a good indication of forest stands preferred by Black Grouse as feeding habitat during winter.

Several studies have pointed to the importance of young forest and birch in the winter habitat of Black Grouse (Seiskari 1962, Sørensen 1978, Toverud 1981). Sørensen (1978) and Toverud (1981) reported a 20% horizontal coverage of birch in the conifer forests preferred by Black Grouse. In our study area, Black Grouse preferred dense stands of tall birch for feeding. Very few heaps of droppings were found in forest stands with fewer than 150 birch ha^{-1} higher than 8 m. The low usage of the south side of the valley, as indicated by a low number of heaps of droppings and few recordings of instrumented birds, is correlated with the removal of hardwoods by herbicides and selective logging. The age structure of the forest was similar on the two sides of the lake, suggesting that selection of one side could not be due to a higher proportion of a preferred age class of trees. Nor could the location of the lek be the reason because the Black Grouse had to fly over the lake from the display ground to the preferred side of the valley. However, due to considerable differences in general vegetation and landscape features between the two sides of the lake (see above), differences in the use by Black Grouse of the two sides of the lake may not have resulted solely from differences in birch abundance.

The importance of catkins in the diet of Black Grouse is well documented (Kaasa 1959, Semenov-Tjan-Shanskij) 1960, Pulliainen 1982, Sodeikat and Strauss 1990). Birch catkins were preferred to birch twigs and buds and also to needles of Scots pine (Pulliainen 1982). Catkins were also preferred by other grouse species that feed on deciduous trees in winter, including Hazel Grouse (Swenson 1991) and Willow Ptarmigan *Lagopus lagopus* (Brittas 1984, Myrberget and Aarbakken 1987). The dominance of birch catkins also during the winter with little snow is in accordance with studies showing that Black Grouse may feed extensively on catkins in the autumn before the arrival of snow (Kaasa 1959, Pulliainen 1982). Catkins have a higher digestibility and contain more protein than other food plants taken in winter (Pulliainen and Iivanainen 1981, Brittas 1984, Andreev 1988). However, increased feeding on bilberry when available may indicate that a diet consisting of different plant species and plant parts could provide a better nutritional balance than feeding on catkins only.

Black Grouse chose the highest trees with the widest canopies and most catkins as feeding trees. Similarly Hazel Grouse preferred to forage in tall alder trees *Alnus incana* rich in catkins in winter (Swenson 1991). Due to the intercorrelation between tree height, canopy width/branch thickness and number of catkins, Black Grouse may obtain not only abundant food but also stable branches for sitting and a high vantage position and therefore better possibilities to detect predators when selecting the highest trees within a stand.

In most of the winter, Scandinavian Black Grouse have a short feeding period in the morning and then seek shelter in snow burrows for the rest of the day. Roosting in snow burrows is apparently energetically advantageous (Marjakangas 1992). Further, survival may be increased by making birds less vulnerable to predation (Marjakangas 1992). In 1991-92, more than 70% of our radio-collared birds were killed (Spidsø unpubl.). The highest predation was recorded during the snow-free winter, with Goshawks *Accipiter gentilis* as the main predators. This is a high mortality rate and may have been caused by the birds being more vulnerable to predation. During winters with normal snow cover, birch trees rich in nutritious catkins of large volume may satisfy the forage requirements of Black Grouse within a short time. This may allow the birds to seek shelter in the snow for most of the day and thereby reduce exposure and the risk of predation.

Implications for forest management

To offer Black Grouse preferred winter habitat, forest stands should include at least 150-200 birch trees ha^{-1} taller than 8 m. Our study shows that tall birch trees with wide and long canopies and a rich supply of catkins are selected as feeding trees. To achieve vigorous growth and a large canopy, trees must grow under good light exposure. Therefore, birch should be left in clumps and small pure stands rather than single trees tightly surrounded by dense coniferous forest. Further, birch should be left as edge trees towards openings such as mires and rock outcrops. To achieve the quality of good grouse habitats, the structure of the forest must be planned at an early stage. This requires particular consideration when control of deciduous brush is done with herbicides sprayed from helicopter. It can more easily be done when brush is controlled either mechanically or chemically by a ground crew. In this way, it is possible to control the brush more selectively so as to let enough trees grow to satisfy the habitat requirements of Black Grouse.

Our study shows what type of birch trees Black Grouse may prefer, but does not tell if these are a prerequisite for dense populations of this species. This may be tested by comparing densities of Black Grouse with forest composition over a larger area (Hjeljord and Fry 1994).

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Summary

Use of forest stands by Black Grouse in winter was estimated through counting and mapping heaps of droppings left by birds roosting in the snow holes. Droppings were also analysed to determine the birds choice of forage plants in winter. Trees fed on were identified by droppings on the ground underneath the trees. Birch catkins dominated Black Grouse diet during a winter with normal snow cover and also during a winter with sparse snow, but twigs of bilberry increased in importance when snow was sparse. During the winter with normal snow cover, Black Grouse used forest stands more when the birch trees were higher than 8 m. Few stands with less than 150-200 birch trees ha^{-1} were used. Compared to control trees, birch trees used by Black Grouse were taller, had larger canopies and more catkins.

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The size of Black Grouse lek populations in relation to habitat characteristics in southern Norway

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Introduction

Several studies have documented preference of the Black Grouse *Tetrao tetrix* for the young stages of boreal forest (Seiskari 1962, Angelstam 1983, Kolstad et al. 1985). However, in spite of an increased area of young forest as a result of forestry management practices, Black Grouse appear to have declined in numbers in Scandinavia in recent decades (Sørensen 1979, Järvinen and Väisänen 1984, Lindén 1989). This may indicate that the quality of the new forests produced by modern silviculture does not meet the requirements of this species. Järvinen and Väisänen (1984) have shown that since the 1940s the Black Grouse in Finland has decreased more than the other grouse species. They suggest this may be due to cutting of birch forest, the preferred winter forage of Black Grouse (Kaasa 1959). A preference for forest stands with abundant birch is documented in several studies (Seiskari 1962, Toverud 1981, Brittas et al. 1987, Eggestad et al. 1988). Hjeljord et al. (1995) also found that during winter Black Grouse preferred forest stands with at least 150-200 birch trees/ha taller than 8 m.

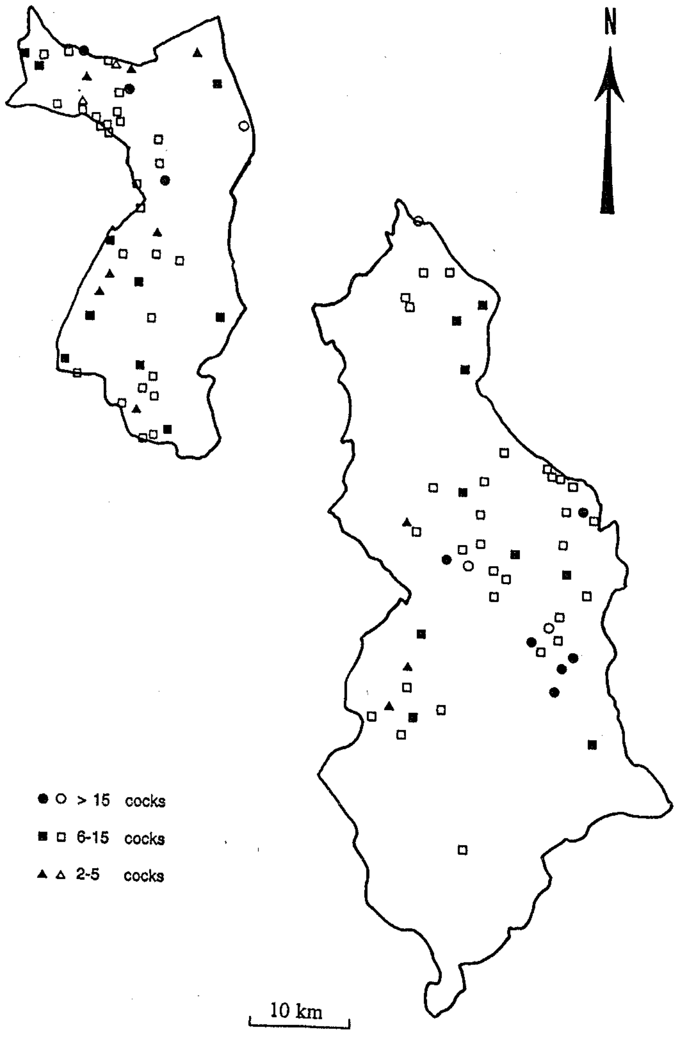

Fig. 1. Distribution of Black Grouse leks within two municipalities of Akershus county, southern Norway. Filled symbols are leks selected for habitat study. Large areas with no leks are unsuitable grouse habitat.

These findings may indicate that the proportion of birch in the forest is a limiting factor for the abundance of Black Grouse. To investigate this hypothesis, we compared the number of displaying male Black Grouse on leks in southern Norway with the proportion of birch in the surrounding forest. We also investigated the importance of other habitat characteristics, including areas of old and young forest, mire, agricultural land, and age-class heterogeneity of the forest. The project was part of a larger study of the ecological effects of glyphosate application.

Study area

The area selected for the field study (Akershus county) was located in southern Norway 50-100 km from the coast and 100-800 m ASL. The area belonged to the boreo-nemoral zone (Abrahamsen 1984), and most of it was forested, mainly with spruce *Picea abies* and pine *Pinus sylvestris*. Mature forest was harvested by clearcutting, and birch *Betula pubescens* and *B. pendula* and rowan *Sorbus aucuparia* dominated on clearcuts in the first years after logging. Clearcuts were small, usually <10ha. The grouse habitats selected for this study covered c. 2100 km² within 4 municipalities of Akershus county.

Methods

A total of 118 Black Grouse leks was found during the first year of the study, which we believe is more than 90% of all leks within the area. Only traditional leks where males had been displaying for many years were included in the study. Counts of displaying males were carried out by members of local hunting clubs during the most intensive song period in the last two weeks of April and the first week of May. The leks were divided into 3 groups according to number of displaying males: small (2-5), medium (6-15) and large

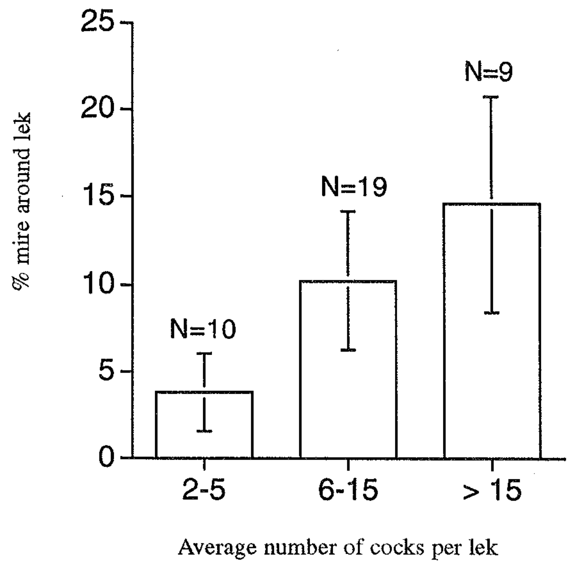

Fig. 2. Average percentage of mire within 1.5 km of leks with 2-5, 6-15 and >15 displaying cocks, Akershus country, southern Norway.

(>15). Within the three groups, 38 leks (10 small, 19 medium and 9 large) were selected as representative of the range of variation for detailed monitoring of lek size and for closer surveys of habitat characteristics over a four-year per-iod (1989-92) (Fig. 1).

Males of Scandinavian Black Grouse appear to stay within 1.5 km of their lek arena throughout the year (Angelstam 1983, Kolstad et al. 1985, Willebrand 1988, Eggestad et al. 1988). We therefore related average number of displaying males on each of the 38 leks to habitat characteristics within 1.5 km around the lek arena. These circular 7.065 km^2 areas are called lek habitats. In some areas, several leks were located close together, giving a high bird density. We chose large leks within areas of high bird density and small leks within areas of low bird density using the following procedure: leks belonging to the small and medium groups were chosen so that the combined number of males on the lek together with males on leks within a 1.5 km circumference did not jointly exceed the number of birds set for each group (5 for small leks and 15 for medium leks).

To analyse forest and landscape characteristics of lek habitats, we used coloured, infra-red aerial photographs at 1:15,000 scale. A stratified-random point-sampling technique (Clarke 1986) was used to quantify the percentage cover of selected habitat classes. The photographs of lek habitats were covered with transparent film and an equal number of points was located at random within 2x2 cm sub-sections of each transparency. The proportion of each habitat type was computed by counting the number of points within different habitat types. By using a sample of 360 points, we obtained a 6-7% standard error. Height of trees (h) was used to indicate the age of forest classed as "old birch" (>8 m), "young birch " (5-8 m), "birch plantations" (1-5 m), "old conifers" (>15 m), "young conifers" (5-15 m), "conifer plantations" (1-5 m), and clearcuts (<1 m). We also recorded single birch trees, mires, lakes, agricultural land and roads.

Landscape heterogeneity for each lek habitat was assessed by sampling with linear transects; four equally spaced parallel transects were aligned N-S and four E-W. Within each cell (25x25m) of each transect, habitat was recorded as young forest and plantations, old forest, open water, mire, clear cut, or other (mainly agricultural land). A landscape diversity index which responds well to the size of habitat patches is the runs test (Wratten and Fry 1980); this was applied to each aerial photograph and used as a measure of landscape heterogeneity. In practice, each of the eight transects (100 units) was analysed separately and the results averaged for the whole photograph.

The relationship between the average size of each lek population and habitat variables was tested by simple linear regression and by step-wise multiple regression analysis.

Results

On the 38 leks selected for habitat analysis, numbers of displaying males were monitored for 4 years on 16 leks, for 3 years on another 16 leks, and for 2 years on 6 leks. The average numbers of males on the 16 leks monitored in the four years 1989-1992 were 9.6, 11.5, 8.8 and 8.3. The numbers of leks in each of the three size groups did not change between years.

The sizes of lek populations increased with the area of mire within the lek habitat (Fig. 2). Area of mire varied between 1% and 21% ($\bar{x}$ = 7%) within lek habitats. No other single habitat factor showed a clear relationship with the number of males on the leks (Table 1). Step-wise multiple regression analysis did not improve correlations above those obtained by analysing each habitat character separately. Areas of young forest/plantation varied between 14% and 51 % ($\bar{x}$ = 31%) and of old birch forest between <1% and 7% ($\bar{x}$ = 4%) within lek habitats, but neither showed a clear relationship with size of lek populations. Four leks with less than 1% of birch in the combined classes "old" and "young" forest, "plantations" and "single trees" had averages of 5, 11, 13 and 17 displaying males over the four years. The lek with the largest area of birch trees above 8 m was also one with a high percentage of young forest, yet it held only 4 displaying males.

Our analysis of landscape heterogeneity showed that the average units of habitat blocks within lek habitats measured from 100 to 250 m across. However, although the sites displayed a wide range of landscape heterogeneity there was no clear relationship between this variable and lek populations ($r^2 = 0.034$, $p = 0.27$).

Discussion

Given our method of sampling (including only communal leks), the lack of correlation between area of young forest and size of leks should be expected: Angelstam (1983) found communal leks only in patches of young forest larger than approximately 1 km^2 and within such patches there was no correlation between densities of male Black Grouse displaying on communal leks and patch size. A significant

Table 1. Correlation coefficients between numbers of displaying cocks on leks and percentages of different habitats within 1.5 km around each lek.

Habitat (height of trees)	Correlation coefficient
Old coniferous forest (>15 m)	0.07
Young coniferous forest (5-15 m)	0.009
Conifer plantations (1-5 m)	-0.146
Clearcuts (<1 m)	0.009
Old birch forest (>8 m)	-0.097
Young birch forest (5-8 m)	-0.097
Birch plantations (1-5 m)	0.191
Mire	0.625*
Lakes	0.295
Arable farm	-0.339
Roads	-0.216
Size of lek-arena	0.410

* Significant relationship, $p < 0.05$.

correlation between patch size of young forest and density of male Black Grouse in Angelstam's study was evident only when **both** solitary displaying young cocks (displaying on young forest patches below 1 km^2) **and** older birds on communal leks were included in the analysis.

Within all lek habitats selected for our study, the total area of young forest was greater than 1 km^2. Although interspersed with some old forest, the area of this habitat apparently still qualified as continuous patches of suitable Black Grouse habitat. However, as the number of males on leks varied between 2 and 27, the quality of these patches as Black Grouse habitat may have varied considerably. We expected winter forage provided by mature birch trees to be one such quality element (Hjeljord et al. 1995). But although the areas of birch forest with trees above 8 m varied between 1-7% of the lek habitat, we found no correlation with the size of lek populations. The positive effect of birch on Black Grouse habitat preference is well documented (Seiskari 1962, Toverud 1981, Brittas et al. 1987, Eggestad et al. 1988, Hjeljord et al. 1994), but in our study area the amount of winter food provided by mature birch trees did not appear to be an important factor determining size of Black Grouse lek populations. It is of interest in this connection that Black Grouse populations in parts of Finland have continued to decrease in spite of extensive artificial winter-feeding (Marjakangas 1987).

Because our data do not support the hypothesis on the importance of winter food, an alternative explanation might be that size of male lek populations correlates with the quality of summer breeding habitat and brood survival. Young males tend to be poor dispersers and most recruit into the nearest lek (Willebrand 1988, Baines 1995).

Few studies have been published on brood habitats of Scandinavian Black Grouse, but older successional woodland stages on poorly drained ground with good vertical cover and a continuous layer of *Vaccinium* spp. appear important (Kolstad et al.1985, Brittas et al.1987). Also a preference for edges between forest and mire as feeding habitat (Kolstad et al. 1985), and for pine bogs as nesting habitats (Storaas and Wegge 1987), have been documented. In our study, the only significant correlation found was between size of lek populations and area of mire. Because Scandinavian Black Grouse avoid open mires except during the lek season (Brittas et al. 1987), this may indicate that the ecotone between forest and mire is a better brood habitat for Black Grouse than the ecotones between different age classes of forest. From all this, the correlation between lek size and area of mire may be due to better average breeding success of Black Grouse in areas with bigger mires than in areas without or with only small mires.

Helle and Helle (1991) compared recent changes in Finnish grouse populations with changes in forest structure. They concluded that the decline in Black Grouse seemed to be wholly independent of changes in forest structure. They suggested that this may be because their analysis lacked data to describe forest fragmentation at the landscape level. In our study, however, analysis of landscape heterogeneity did not help to explain differences in size of lek populations.

Conclusion

Although the quantity of potential Black Grouse habitat increases with area of young successional stages of the boreal forest, there remains a need for a better understanding of the elements which improve habitat quality. Secondary forest produced by modern silviculture, in contrast to naturally regenerated forest, tends to develop a very dense canopy which shades out ground vegetation. Better knowledge of the importance of such changes in micro-habitats on the growth and survival of adult and young Black Grouse will be important for the development of forestry guidelines for grouse management.

Summary

Colour infra-red aerial photographs at 1:15,000 scale were used to analyse the habitat characteristics of forested landscapes within a 1.5 km radius of 38 Black Grouse leks in southern Norway. A stratified random point-sampling technique was used to quantify the cover of different types of forest, clearcuts, lakes, mires, roads, human dwellings and

cultivated fields. Habitat heterogeneity was assessed by sampling along linear transects. The area of open mire was the only habitat component to show a significant positive relationship with the size of lek populations. There was no correlation with area of preferred winter habitat such as old birch forest and there was no clear relationship between lek populations and habitat heterogeneity. Quality of brood habitat may be the most important determinant of size of lek populations of Black Grouse in the area studied.

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Energy costs of incubation in Rock Ptarmigan *Lagopus mutus* in Switzerland

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Introduction

Populations of grouse, like other ground-nesting birds, commonly lose up to half of their clutches due to predation. A female's loss in fitness is greater from this single factor than from any other (Bergerud and Gratson 1988), and presumably one of the most important goals of a breeding grouse female should be to prevent detection of the nest. To succeed, the bird has to face several problems to which it should find optimal solutions. Factors such as ground cover, predator abundance, breeding density, climatic and microclimatic conditions or the possibility to re-nest may affect nest location. Once a female has laid and started incubation it is confronted with a different problem; uncovered eggs are usually much more conspicuous than the incubating female and a moving female is much easier to detect than a motionless one. The best strategy to avoid detection of the nest during incubation would be to stay motionless on the eggs and not leave the nest at all. Presumably this is not possible, especially in species like the ptarmigan where the female does all the incubating over the 21-day incubation period and is not fed by the male. She needs to leave the nest to feed and defaecate. Energy intake through feeding is especially important to minimize mass loss during incubation. The female still needs to use body reserves during the first two weeks after hatching (Steen and Unander 1985). Leaving the nest frequently or for long periods may increase the risk that a predator detects the nest, and the female must balance the benefits of energy intake with predation risk.

In this study, I examine the energetic costs of the time the female spends away from the nest and investigate the following points:

(i) The amount of energy needed for incubation.

(ii) The relation between the energy spent during incubation and the pattern of incubation.

(iii) The efficiency of energy gain away from the nest.

Methods

Field investigations were done in summer in 1992 and 1993 at Grindelwald (Switzerland, 2000 m ASL). Sensors to measure physical parameters and the presence of the female were installed at the nests of three radio-tagged Rock Ptarmigan females *Lagopus mutus helveticus* during egg-laying. Egg temperature was measured by putting a thermistor (ø 2 mm, 2252 Ω at 25°C) through a hole made at the pointed end of a freshly laid egg. The thermistor was placed in the middle of the egg, the egg was then injected with an antibiotic and an antimycotic, the hole was sealed with glue and the egg was put back in the nest. Eggs were weighed (precision 1/10 g) at the beginning of incubation and shortly before hatching. Ground temperature was measured by a soil temperature probe (ø 4.8 mm x 125 mm from Delta-T-Devices, England) 5 cm deep parallel to the surface, pointing to the centre of the nest. Air temperature was measured in a solar radiation screen 20 - 30 m away from the nest and 2 m above ground. Additionally, the air temperature was measured unshielded at the rim of the nest with a similar probe to that used for ground temperature. All temperatures were accurate to ± 0.2 °C. Global radiation was measured at the nest with a photodiode with a spectral bandwidth from 400 to 1000 nm. Wind speed was measured 20 - 30 m away from the nest and 2 m above ground with an anemometer from Delta-T-Devices. Rainfall was measured at the same place with a tipping bucket raingauge and summed over 10 min. The presence of the female on the nest was measured with an infra-red barrier every 10 sec. Egg temperature was measured at intervals of 1 min. The other parameters were measured every 10 min. All the measurements were collected by a data logger which also controlled the infra-red barrier .

Costs of incubation

I assume that a breeding female uses energy only for two things: to maintain resting metabolic rate (RMR) and to keep the eggs warm.

During incubation, the air temperature ranged from -0.1 to 25.9 °C (with one exceptional day of 32.9 °C). This lies within the thermoneutral zone of Rock Ptarmigan in summer plumage, which have a RMR of 586.989 $kJ*kg^{-1}*day^{-1}$ (Mortensen and Blix 1986). Thus RMR probably stayed constant throughout incubation. The amount of energy that the female needed in addition to RMR in order to keep the eggs at a stable temperature under different climatic conditions is defined as 'costs of incubation'. This amount is at least equal to the amount that the eggs lose to the ground. It depends on the egg mass of the clutch (m_e), the specific heat capacity of the eggs (c_e) and the heat transfer from the eggs to the surrounding ground, which is determined among other things by the difference between egg temperature, ground temperature and a constant c_{ec}. This constant is different for different nests. C_e was measured in the laboratory using a calorimeter and found to be 3.522 $kJ*kg^{-1}*^0K^{-1}$ (+/- S.D. 0.059) (Table 1). In order to determine c_{ec}, I covered the nest with a small bag filled with polystyrol pellets (ø 2mm) after the female had left the nest so that the eggs would only lose heat to the ground. I measured the ground temperature and then every minute the cooling of the eggs for 15 - 20 min. To these data (that is the diminishing difference between egg and ground temperature) I fitted a

Table 1. Specific heat capacity (c_e) of fresh Rock Ptarmigan eggs as measured in the laboratory using a calorimeter.

Number of measured eggs	Weight (g)	c_e ($kJ*kg^{-1}*^0K^{-1}$)
1 clutch with 5 eggs	105.4	3.588
1 clutch with 5 eggs	102.8	3.525
1 egg	20.1	3.427
1 egg	20.1	3.547

Table 2. Parameters of the curves $f(x) = \exp(a+bx)$ fitted to the cooling of three different clutches which were covered with a small bag filled with polystyrol pellets in order to inhibit heat loss to the air. The experiments were done in the first half of the incubation. d_{yx} is the difference between the measured value and the one calculated as f(x). Mean error = $\mathrm{SQR}(\Sigma d^2_{yx}) * 1/n$.

Nest	a	b ($=c_{ec}$)$*10^{-3}$	mean error (+/- ^{0}C)
A	3.10354	-4.9148	0.035
	3.18656	-4.8168	0.029
B	2.88903	-15.6889	0.066
	2.96277	-16.2970	0.058
C	2.92447	-5.8677	0.004
	2.91439	-5.4965	0.004

curve of the form $f(t) = \exp(a+bt)$. Because $f'(t) = b * f(t)$, b tells how much the clutch cools down per time interval and per ^{0}K difference between egg and ground temperature. I then put $b = c_{ec}$ with the dimension $^0K*^0K^{-1}*min^{-1}$ and called it 'cooling rate of covered eggs' (c_{ec}). At all three nests I conducted this experiment twice in the first half of the incubation. The mean of c_{ec} for the different nests was found to be $-4.8658*10^{-3}$, $-15.9930*10^{-3}$ and $-5.6821*10^{-3}$ (Table 2). The energy needed to incubate any of the three nests, dependent on egg and ground temperature could now be calculated as:

$$Q = dtemp * c_{ec} * c_e * m_e * dT$$

dtemp = difference between egg and ground temperature.

c_{ec} = cooling rate of the clutch

c_e = specific heat capacity of Rock Ptarmigan eggs

m_e = egg mass of the clutch

dT = time

In the field, I recorded ground temperatures of 6 - 20 ^{0}C. To keep the eggs under these conditions for 1h at a normal incubation temperature of 35 ^{0}C, the female needed, according to my equation, 2.700 - 5.221 kJ in nest A, 6.864 - 13.270 kJ in nest B and 2.815 - 5.442 kJ in nest C (Fig.1). This means that low ground temperatures can almost double the cost of incubation. The same is true for poor insulation of the nest as in the case of nest B, where in some places the eggs touched the bare ground. The costs of incubating clutch B were twice as high as for the other two nests, even though it was the lightest with a weight of 135.1 g compared to 175.1 g for clutch A and 156.3 g for clutch C.

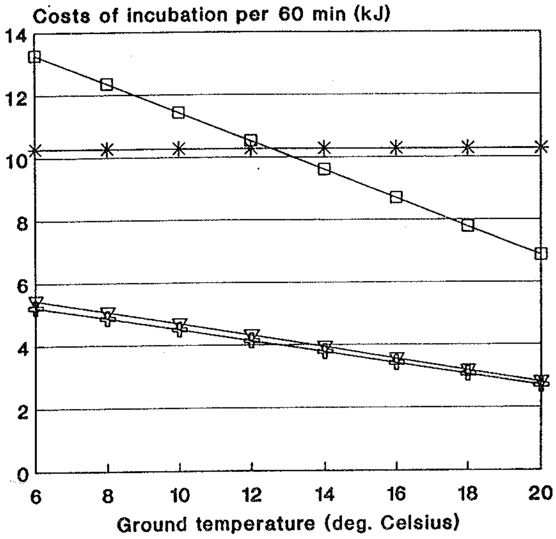

Fig. 1. Amount of energy needed to incubate three different nests at ground temperatures from 6 - 20°C and an egg temperature of 35°C. The resting metabolic rate (RMR) of a Rock Ptarmigan hen in summer plumage and with a bodymass of 420g is shown for comparison (Mortensen and Blix 1986).

Length of time the female was off the nest and energy spent during incubation

The energy spent during incubation consists of the 'costs of incubation' and the amount of energy spent for the resting metabolism. The energy input during incubation consists of energy gained by conversion of body mass and of energy that the female gains as food during the time off the nest.

Once incubation starts, the energy output depends solely on the climatic conditions. The female can only manipulate the intake side. The amount of body mass to be converted into energy is limited and I assume as a first step that the female uses it in a linear way, that is to say, every day the same amount. Then I expect the female to vary the total duration away from the nest according to the change in energy output. I tested this prediction in two ways with the data from nest A and C. (Nest B was excluded from further analyses because there were measurements of time off the nest from only two disturbance-free days at this nest.)

(i) I calculated the 'costs of incubation' for specific days and compared this to the total time the female left the nest on that day. No significant correlation was found (Fig.2).

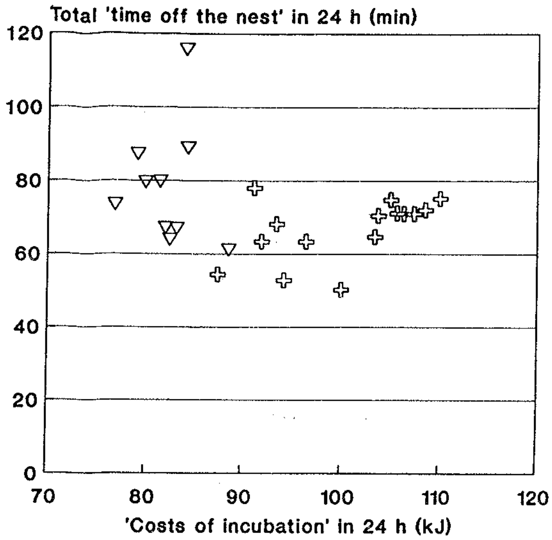

Fig. 2. Total duration of times off the nest during specific days of incubation in relation to the total 'costs of incubation' on that day.

(ii) I estimated the whole energy output, that is the 'costs of incubation' and the RMR for specific days, and compared this to the total time the female was off the nest on that day. RMR is usually given per kg. Therefore it has to be multiplied by the weight in order to get the actual RMR of a specific individual, but the weight was measured only once during incubation to minimize disturbance. I therefore estimated the weight of the females on a specific day in the following way. Wild Svalbard Ptarmigan *Lagopus mutus hyperboreus* lost 17.2% of their weight during incubation and Willow Ptarmigan *Lagopus lagopus* 16.2% (Gabrielsen and Unander 1987). I used a value of 17% in this study and extrapolated the weight of the female on the different days of incubation from the one measurement made. There was no significant correlation between the total amount of energy spent during a day and the total time off the nest on that day (Fig.3). But there was a significant correlation between the total energy spent in one day and the day of incubation (Fig.4). This was due to the diminishing weight of the female which led to a lowering of the RMR by 2.161 kJ*day of incubation^{-1} at nest A and 2.134 kJ*day of incubation^{-1} at nest C. This overrode the changes in the 'costs of incubation' due to the changes in ground and egg temperature.

Efficiency of energy gain when the female was off the nest

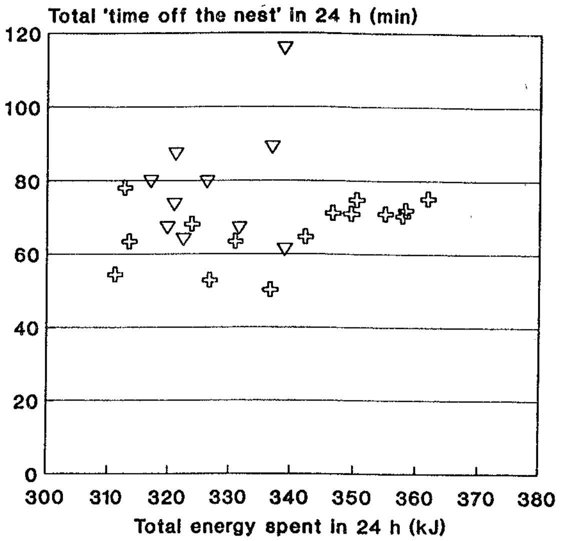

Fig. 3. Total duration of times off the nest during specific days of incubation in relation to the total amount of energy spent, that is the 'costs of incubation' plus the resting metabolism on this day.

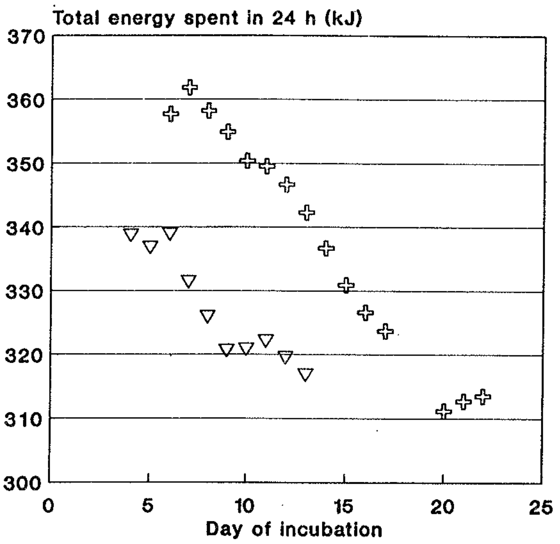

Fig. 4. The total amount of energy spent (that is the 'cost of incubation' plus the resting metabolism) on different days of incubation.

Efficiency is defined as amount of energy that the female gained per minute while off the nest feeding instead of continuously incubating. On the plus side of the energy budget when off the nest is the energy gain from feeding plus the energy which the female would spend otherwise on incubation. On the minus side is the heat loss of the eggs, the energy used to fly to the feeding area and back and the energy used for walking and feeding while at the feeding area. I now calculated the change of efficiency with increasing time off the nest using data from nest A for which there are measurements over the entire incubation period.

The plus side of the energy budget

I did not directly determine the amount of energy in the food ingested because this would have been beyond the possibilities of this study (but see among others Andreev 1987, Gasaway 1976, Moss 1973, 1983). Instead, I estimated it from the following equation which describes the energy budget of the female during incubation:

Total Resting Metabolism (TQ_{rm}) + Total Costs of Incubation (TQ_{ci}) = Total Energy gained by Conversion of Body Mass (TQ_{bm}) + Total Energy Gained during 'time off the nest' (TQ_{tn}).

I have already showed how I calculated resting metabolism, the costs of incubation and the weight loss during incubation. There are reasons to assume that Rock Ptarmigan in the Swiss Alps do not put on fat as reserves (A. Bossert and N. Zbinden, pers. comm.). The same is true for Rock Ptarmigan in northern Norway where body fat never contributes more than 2.7% to the total body weight at any time of the year (Mortensen, Nordøy and Blix 1985). From this, I took the weight lost during incubation as 2.7% fat with a caloric equivalent of 32.238 $kJ*g^{-1}$ (Mortensen and Blix 1985) and the rest as protein with a caloric equivalent of 20.096 $kJ*g^{-1}$ (Kleiber 1975). From the above equation, three parameters are now known and the total energy gained during the 'time off the nest' can be calculated as follows:

$$TQ_{tn} = TQ_{rm} + TQ_{ci} - TQ_{bm} = 4890.499 \text{ kJ} + 1944.995 \text{ kJ} - 1664.537 \text{ kJ} = 5170.957 \text{ kJ}$$

The female on nest A gained this energy in a total of 20.32 h 'off the nest'. That means she gained 4.241 kJ per min off the nest (Q_{tn}). For comparison, I derived the same measure from published data (Gabrielsen and Unander 1987) and found it to be 5.452 and 4.539 kJ per min off the nest (Svalbard and Willow Ptarmigan, respectively).

The minus side of the energy budget

Heat loss of the eggs: I used the measurements of eight instances during the first ten days of incubation when the hen left the nest under conditions that were typical for the early morning, viz air temperature around 4 °C, ground temperature of 8.5 °C and radiation <100 watt per m^2. To the diminishing difference between egg and air temperature, I fitted a curve with $f(t) = A * \exp(bt)$ where t is the time since the female left the nest. A is the difference between egg and air temperature at t=0 and b is the cooling rate for uncovered eggs (c_{eu}). The mean of c_{eu} was -20.8833*10-3 $^{o}K*^{o}K^{-1}*min^{-1}$ (S.D. ± $2.3703*10^{-3}$) (Table 3).

The energy used to fly to the feeding area and back: All six females that I observed at nests normally flew to nearby feeding grounds. I estimated the flight time to be 5 sec each way. Masman and Klaassen (1987) predicted avian flight cost (Q_{fc}) from an equation based on published data on flight costs in 14 species (body mass 3.8 - 1000 gr):

$$Q_{fc} = 17.36 * M^{1.013} * b_w^{-4.236} * s_w^{1.926}$$

For this study, I used the following values from our own measurements on Rock Ptarmigan: M = body mass = 411 g; b_w = wing span = 54 cm; s_w = wing area = 524 cm^2. This results in Q_{fc} = 61.3 $J*sec^{-1}$.

The energy used for walking and feeding: Gabrielsen and Unander (1987) showed that the mean heart rate of wild Svalbard Ptarmigan and Willow Ptarmigan was 155 / 138 bpm while resting and 205 / 224 bpm while walking with a linear relation between heart beat and metabolic rate. So I estimated the energy used for walking and feeding to be twice the resting metabolic rate, that is for a female with the body mass of 411 gr., 335 $J*min^{-1}$.

Table 3. Parameters of the curves $f(t) = A * \exp(bt)$ fitted to the cooling of the eggs in nest A at eight instances when the female left the nest in order to go feeding. d_{yx} is the difference between the measured value and the one calculated as f(t). Mean error = $SQR(\Sigma d^2_{yx}) * 1/n$.

A (exp())	b (=c_{eu})*10^{-3}	mean error (+/- °C)
3.3712	-20.952	0.153
3.2638	-24.8315	0.175
3.3247	-22.8519	0.142
3.4275	-17.4911	0.111
3.4194	-18.1666	0.112
3.2806	-18.8359	0.090
3.4473	-21.8184	0.148
3.4040	-22.1185	0.133

Efficiency

The efficiency (E) can now be calculated as:

$$E = (Q_1 + Q_2 - Q_3 - Q_4 - Q_5) / t$$

Q_1 = Energy gained by taking up food = $Q_{tn} * t$

Q_2 = Energy saved by not incubating = $B * c_{ec} * c_e * m_e * t$

Q_3 = Heat loss of the eggs = $(A * \exp(c_{eu}*0) - A * \exp(c_{eu}*t)) * m_e * c_e$

Q_4 = Energy used for walking and feeding = $2 * RMR * m_b * t$

Q_5 = Flight costs = Q_{fc} = 0.613 kJ

A: difference between egg- and air temperature;
B: difference between egg- and ground temperature;
ce: specific heat of eggs; cec: cooling rate of covered eggs;
ceu: cooling rate of uncovered eggs;
mb: body mass of the female;
me: mass of the eggs;
RMR: resting metabolic rate;
t: time since the female left the nest.

I calculated the efficiency for every minute off the nest until the eggs would reach 25 °C. This temperature is known as the 'physiological zero' in domestic fowl (for a review see Decuypere and Michels 1992). Egg temperature was set to be 6 °C at the start, ground temperature 8 °C and air temperature 0, 5, 10, 15, 20, 25, or 30 °C. Additionally, I calculated how much energy the female would have gained totally before the eggs would reach 'physiological zero' under the different conditions. This is represented by the area under the curves in Fig. 5.

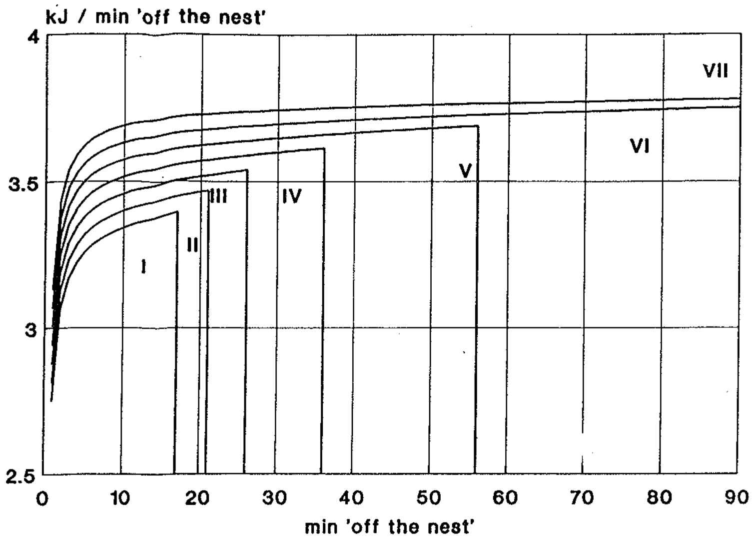

Fig. 5. Change in efficiency of energy gain during times off the nest for air temperatures of 0, 5, 10, 15, 20, 25 and 30 °C (I - VII). Egg temperature at the start was set to 36 °C and ground temperature to 8 °C. The areas under the curves represent the total amount of energy gained until the eggs would reach 'physiological zero' at 25 °C and amount to 54.264 kJ, 67.493 kJ, 87.620 kJ, 122.196 kJ, 198.223 kJ (I - V) and over 325.417 kJ (VI and VII).

At differences between egg and air temperature of 36, 31, 26, 21, 16, 11 and 6 °C, corresponding to an egg temperature of 36 °C and air temperatures of 0, 5, 10, 15, 20, 25 and 30 °C, the female stayed away from the nest for 17, 21, 26, 35, 56 and over 90 min until the eggs reached 'physiological zero'. In this time, she gained 54.264, 67.493, 87.620, 122.196, 198.223 and over 325.417 kJ net energy. Surprisingly, in all instances, she gained net energy already in the first minute off the nest.

At all considered differences between egg and air temperature, the efficiency rose with increasing 'time off the nest', mostly in the first 10 min. At all times, efficiency was higher with a small difference between egg and air temperature than when there is a big difference.

Taken together, this means that taking 'time off the nest' with small differencies between egg and air temperature pays off better right from the beginning and that the amount of net energy that can be gained before the eggs reach 'physiological zero' is much larger at small differences than at big ones.

Discussion

Female Rock Ptarmigan need to find an optimal pattern for time off the nest in relation to energy budget and anti-predator tactics in order to incubate successfully. If we know what an energetically optimal pattern looks like, we can compare this to what females in habitats with different predator species and/or different predator densities actually do. The difference between the two is an indication of how 'expensive' a certain anti-predator tactic is in terms of energy. This can help to understand how anti-predator tactics are shaped or eventually limited by the energy budget of the incubating female.

In this study, I was concerned only with the energetically optimal pattern for time off the nest. By 'pattern', I mean how often, how long and when in the daytime a female leaves the nest. According to my calculations, the female gained net energy from the first minute that it was off the nest, even in very low air temperatures. If the only goal was to gain energy, then the female could leave the nest at any time of the day and as often as it wants. But every time she leaves, she begins with a low efficiency. Therefore, if the goal is to gain energy also as efficiently as possible it should leave the nest as seldom as possible.

Once the female had left the nest it should stay off as long as possible because the efficiency of energy gain increased constantly. The time is only limited by the drop in egg temperature. It is known that Rock Ptarmigan eggs can tolerate a very low ambient temperature and still hatch. Low temperatures may not harm the embryo, but they will certainly stop development and in this way will prolong incubation time. Because on the return of the female I very seldom recorded egg temperatures below 25 °C and never below 22 °C, I believe that for Rock Ptarmigan there is a 'physiological zero' at approximately 20-25 °C which sets a limit to the time that the female should stay away from the nest. The smaller the difference between egg and air temperature and egg and ground temperature is at the start, the longer it will take until this point is reached. My calculations show, that e.g. with a difference of 6 °C between egg and air temperature at the start and a rather low ground temperature of 8 °C it takes more than 90 min to reach 'physiological zero'. Usually, the three females were off the nest and feeding for 40 to 90 min in each 24 h period. From my results, I conclude that the energetically optimal way to spend this amount of time off the nest would be to leave the nest at the warmest time of the day and to stay off until the eggs reach 'physiological zero'. In this way, the females would have to leave the nest only once or twice in 24 h.

Females usually stayed off the nest until the eggs had reached approximately 25 °C, but they did not do this at the warmest time of the day. Each of the three females left the nest 0-2 times during the morning and the late afternoon and regularly once at dawn and once at dusk, when temperature differences were usually high. The easiest explanation for this appears to be that the female, not being able to feed at night because of poor visibility, would have exhausted the food in her crop by dawn and that at dusk she would get sufficient feed to last through the night.

However, Erikstad (1986) observed that incubating Willow Ptarmigan in central Norway regularly left the nest during the night. So it is plausible that Rock Ptarmigan too would be able to feed at night if they chose to do so. With this in mind, my results and observations that incubating Rock Ptarmigan females chose to go off the nest at times which are energetically not optimal can be interpreted as an anti-predator tactic. Depending on the predator species, it could pay to avoid the time when the predator is hunting, even if this would mean leaving the nest at times when the efficiency of energy gain is low.

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Summary

The physical parameters (egg temperature, soil temperature, air temperature, solar radiation, rainfall and windspeed) and the presence of the female on the nest were measured at the nests of three radio-tagged Rock Ptarmigan females *Lagopus mutus* at Grindelwald (Swiss Alps, 2000 m ASL). From experiments at nests during incubation, it was possible to calculate the amount of energy needed to incubate each clutch. It was found to be 2.7 - 13.3 kJ per h depending on ground temperature and insulation of the nest. There was no significant correlation between the energy spent for incubation on specific days and the length of time the female was off the nest on that day. It was possible to calculate that once the female had left the nest she gained net energy from the first minute off and that the longer the female stayed off, the higher was the efficiency of energy gain.

I concluded that in order to behave in an energetically optimal way, a female should leave the nest once during the warmest time of the day and stay off until the eggs reached 'physiological zero' at 25 °C. The difference between this optimal pattern and the pattern actually shown by the females is discussed in relation to energy use and anti-predator tactics.

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Home ranges, habitat and dispersal of radio-marked Hazel Grouse in the National Park 'Bayerischer Wald', Germany - Preliminary results

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Introduction

Most investigations on the ecology of the Hazel Grouse *Bonasa bonasia* in Central Europe have been done in forest habitats more or less influenced by man (Bergmann et al. 1982, Zbinden 1979). This three-year project in the National Park Bayerischer Wald, started in 1992, aims to discover how Hazel Grouse used native forests in central Europe as primary habitat and to compare the dispersal strategies of this species with other more mobile grouse *Tetraoninae*.

Material and methods

In July and August 1992, five Hazel Grouse (1 adult male, 2 adult females and 2 juveniles) were fitted with individual radio tags (BIOTRACK Ltd., weight: 8-9 g, frequency: 148 - 150 MHz) in a spruce-dominated forest association 'Aufichtenwald' (one female), and in a mixed deciduous/conifer woodland 'Bergmischwald', a widespread type of forest in the central European mountains, dominated by spruce *Picea abies*, fir *Abies alba*, beech *Fagus sylvatica* and maple *Acer pseudoplatanus* (the other four birds).

The radio-tagged birds were located by cross bearings 5-7 times per week if possible, with a resolution of 25 m. Four birds were monitored for at least two months (Table 1).

Table 1. Hazel Grouse captured in 1992.

No.	Sex	Age	Weight (g)	Date marked	Fate		N locations (until March 93)
051	f	Ad.	372	14 July	Killed by marten	10 Nov	113
052	m	Ad.	382	16 July	Died	6 Aug.	24
053	f 51 d	Juv.	245	26 July	Killed by goshawk	7 Oct.	71
054	m 73 d	Juv.	380	18 August	Killed by goshawk	2 Apr.	149
055	f	Ad.	370	27 August	Alive on	31 Mar 1993	187

Cross-bearings were mapped (scale 1 : 10.000) using a grid of 100 x 100 m. Home range size was determined by counting the number of 100 x 100 m grid cells used and the maximal convex polygon method was used for graphical presentation and overlap analysis. Overlap was defined as the proportion of the second season's home range that was also within the first one. As a measure for habitat use, each radiotracking location was related to a certain habitat type.

Results

1. Home ranges

The home ranges used by three radio-tagged Hazel Grouse in autumn and winter 1992/93 averaged 20 ha. There were only minor differences between individuals, habitat types and seasons (Table 2). Male 054 made occasional sallies around his home range lasting 1-2 or more days. These were not taken into consideration when calculating home-range size; otherwise, this home range would have been much larger (see Fig. 1).

The location of the individual home ranges did not change much from autumn to winter. Overlap was 77.9 % (female 055) and 54.1 % (male 054).

Table 2. Home ranges (ha) of three Hazel Grouse in autumn and winter, as area of grid cells (100 x 100 m), used by the birds.

No.	1 Sept. 30 Nov.	1 Dec. 28 Feb	1 Sept. .28 Feb.
f 051	21*		
m 054	13	17	24
f 055	23	25	32

* killed 10 November

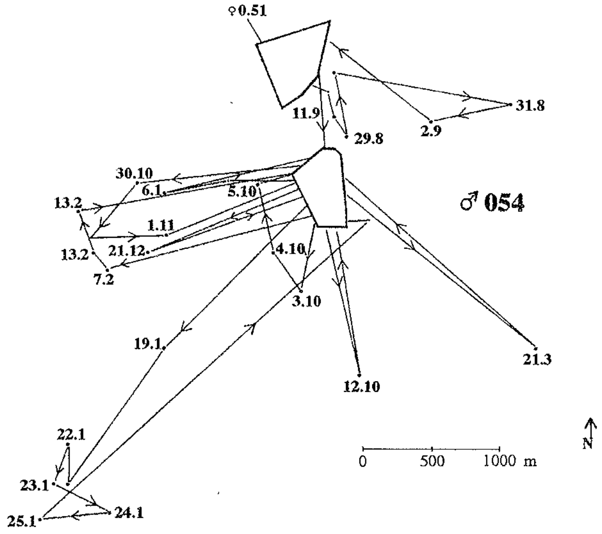

Fig. 1. Dispersal of the first-year male 054 and subsequent excursions into the surrounding forest.

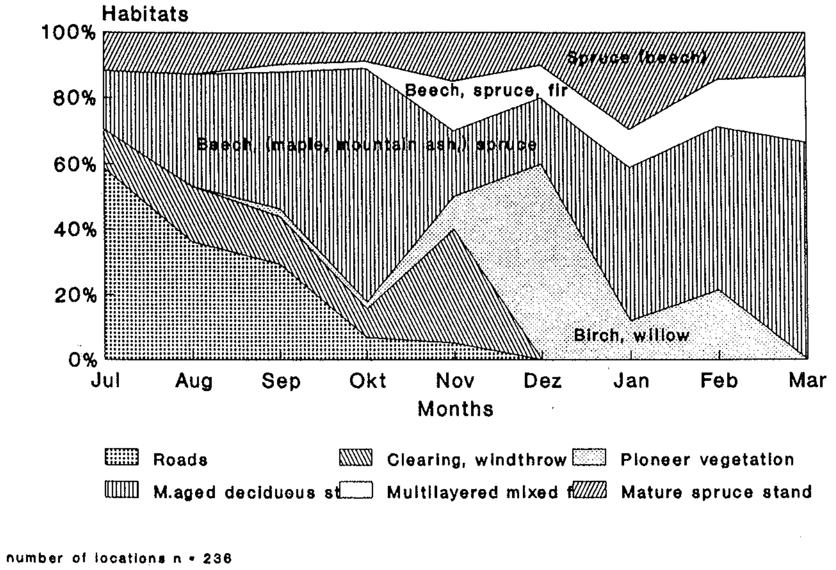

Fig. 2. Habitat selection of two Hazel Grouse, a second-year female (051) and its first-year son (054), in mixed woodland.

2. Habitat use

A. Habitat type 'Bergmischwald' (Fig. 2)
Female 051 and her juveniles used habitats with few trees, such as trails, windthrows and forest gaps, with bilberry *Vaccinium myrtillus* and sandy places for dust-bathing. After the young dispersed in October, there was a marked shift towards denser vegetation cover in spruce and beech/spruce thickets and middle-aged forests with a high proportion (up to 10 %) of birch *Betula pendula*, rowan *Sorbus aucuparia* and aspen *Populus tremula*. A tendency to feed in trees in autumn and a decrease in vegetation cover along trails and on windthrows were responsible for this shift.

Further discussion of habitats used in autumn and winter is based exclusively on the habitat selection of male 054. During November, it used mostly small forest gaps on rocky boulder fields in the otherwise highly structured 'Bergmischwald', where it probably fed mainly on bramble leaves *Rubus fruticosus*. In December, this male was mostly found in a succession area which mainly contained birch, willow *Salix caprea* and aspen. Spruce also was present as undergrowth and along the edges of this area (Fig. 2). In this period, this male mainly fed on birch catkins.

In winter, the mobility of the male decreased so that it was more often encountered in the centre of its home range. It more frequently used thickets, middle-aged forest and multi-layered mixed forest with spruce, beech, fir and maple.

B. Habitat type 'Aufichtenwald' (Fig. 3)
Here, female 055 mostly used mature and middle-aged spruce stands with 5-15 % birch, especially edges next to wind blows, thickets or bogs where the bilberry and cranberry *Vaccinium vitis-idaea* layer was well developed. Here, it could also feed on trees, especially in deep snow. Habitats with few trees (e.g. windthrows and bogs) were important in late summer and early autumn, especially next to woodland

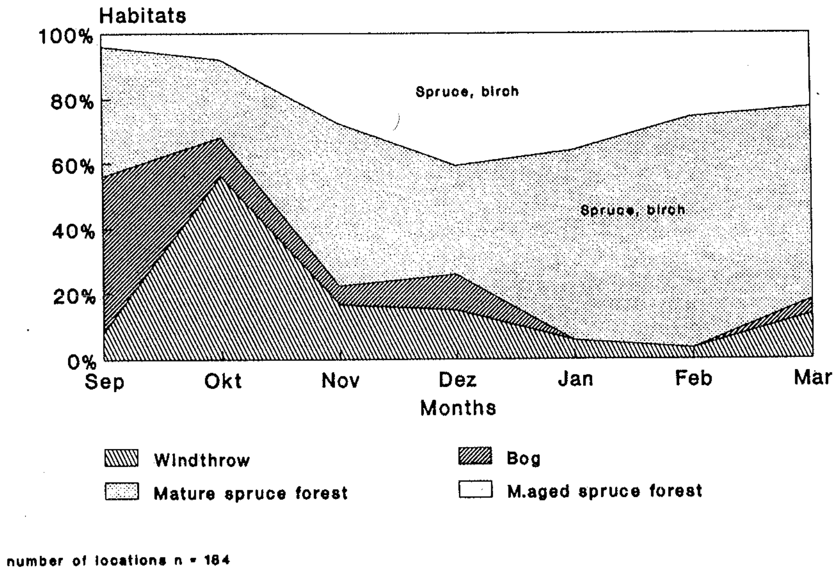

Fig. 3. Habitat selection of a second-year Hazel Grouse (female 055) in spruce-dominated forest.

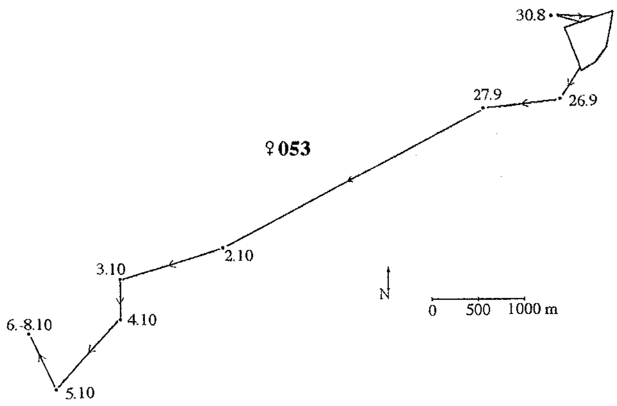

Fig. 4. Dispersal of the first-year female 053.

Table 3. Dispersal behaviour of four first-year Hazel Grouse, two (siblings) in Germany and two in Sweden.

	this study		Swenson 1991b and pers. comm.	
	m 054	f 053	m	f*
Date brood left nest	5 Jun.	5 Jun.	8 Jun.	6 Jul.
First separation from mother	21 Aug.	26 Aug.	8 Sept.	19 Sept.
Age (days)	76	81	93	75
Final separation from mother	5 Sept.	26 Sept.	12 Sept.	19 Sept.
Age (days)	90	111	97	75
Final separation from brood range	11 Sept.	26 Sept.	12 Sept.	19 Sept.
Age (days)	96	111	97	75
Establ. of own home range	12 Sept.	6 Oct.	15 Sept.	26 Sept.
Duration of dispersal (days)	1	11	3	7
Distance of dispersal (km)	0.85	6.8	1.4	0.22

* This female moved c. 900 m south from the site of marking during the dispersal period, then she moved north. Its autumn territory was centred c. 1.2 km north of this farthest point recorded during dispersal.

edges. In summer, the windthrows not only provided much food but also sand-baths. In winter, spruce thickets or middle-aged forests with scarce ground vegetation were important only as sleeping or resting sites.

3. Dispersal

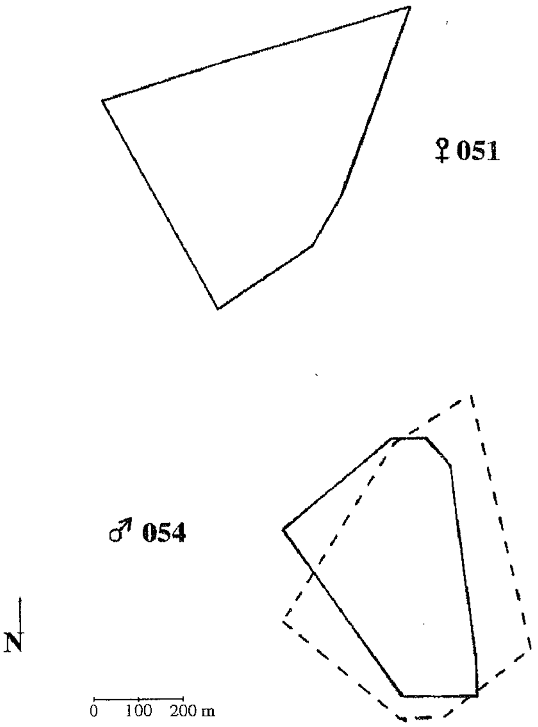

Fig. 5. Home ranges of two Hazel Grouse, a second-year female (051) and its first-year son (054) in autumn (-) and winter (- -) 1992/93 in mixed forest.

The separation from their mother (051) of both juveniles took c. 2-4 weeks from the end of August to the end of September. In this phase, each juvenile was only temporarly found together with either the old female or the other sibling.

At first, excursions of the juveniles hardly left the home range of the mother, but later up to 1-2 km were covered within a few days (Fig. 4).

However, during dispersal, the two juveniles, female 053 and male 054, showed different behaviour (Table 3). Separation from the mother for the first time and final separation took place earlier in the case of the young male than in the young female. Likewise, the process of separation lasted only 2 weeks in the male but 4 weeks in the young female.

The juvenile male also grew faster than its sister (Table 1). While the latter weighed 316 g at an age of 80 - 85 days (27 August), the young male already weighed 380 g at an age of 70 - 75 days (18 August), the usual weight of an adult. The young male was found in its future territory for the first time on 12 September. It gave territorial calls from the first day onwards. On 6 October, the young female found a partner and presumably established a territory in a place where she was caught by a Goshawk *Accipiter gentilis* two days later.

There also were marked differences in the distances of dispersal of the two siblings. The male settled in a neighbouring territory c. 850 m southward, whereas the female passed at least four Hazel Grouse territories (two of them occupied by females, two of them unknown whether occupied or not) before she settled 6.8 km WSW of the parental territory. This is the greatest distance of dispersal of a marked Hazel Grouse reported in the literature. If the

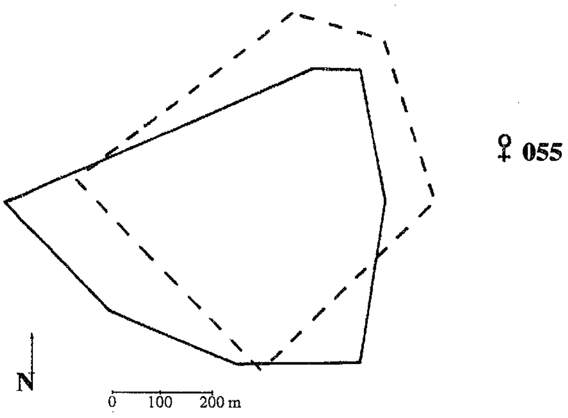

Fig. 6. Home ranges of second-year Hazel Grouse (female 055) in autumn (-) and winter (- -) 1992/93 in spruce-dominated forest.

young female had not been killed by a Goshawk, it possibly would have moved farther (or back). During dispersal, the young birds always moved in vegetation cover such as edges of forest roads or brooks. In this way, they crossed forest areas not usually suitable for Hazel Grouse.

Discussion

Bergmann et al. (1982) considered that Hazel Grouse used different components of their habitat depending on season and time of day.

A seasonal preference for distinct vegetation types and structures was also obvious in the cases of the two radio-tagged Hazel Grouse in the mixed woodlands 'Bergmischwald' in the National Park Bayerischer Wald, but less so in the female monitored in the predominantly coniferous 'Aufichtenwald'. In the latter case, the different structural elements of Hazel Grouse habitat were more intermingled, while in the study area in the 'Bergmischwald' these elements were separate.

While in the 'Aufichtenwald' the three major needs, vegetation cover, summer food and winter food, could be satisfied within one habitat type, in the 'Bergmischwald' it was necessary to visit differently structured parts of the home range for each component.

The size of these home ranges (Figs. 5 and 6) generally agreed with the findings of other comparable investigations in the Black Forest (Germany) and in Sweden (Lieser 1991, Swenson 1991a). Perhaps there is a natural maximum size for home ranges of Hazel Grouse, with the birds unable to use or defend larger areas, independent of habitat type.

The young male 054 and the young female 053 showed big differences in their dispersal. Two radio-marked juveniles in Sweden showed a similar dispersal behaviour (Table 3), but the young female was able to establish a territory near to the brood range (after it had initially moved c. 1.2 km during dispersal), because its mother had left this area (Swenson 1991b). The possibility of different sexual strategies for dispersal will be investigated further.

After successful settlement, the male 054, which did not find a partner until the following March, made many excursions lasting one or more days into the surroundings of his terrritory. These excursions possibly helped to find new females and/or unoccupied or better territories, which are often occupied by new Hazel Grouse within short periods (Swenson 1991a).

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Summary

Five free-living Hazel Grouse (1 adult male, 2 adult females and 2 juveniles) were radio-marked in two different habitats of the national park 'Bayerischer Wald', Germany. Between July 1992 and March 1993, 544 re-locations were taken.

Home ranges of these Hazel Grouse in autumn, described as effectivly used range, were 21 and 23 ha (females) and 13 ha (male). There were no differences in the sizes of home ranges between habitats.

But in a middle-aged (30-70 years), partially mature (> 110 years) and multi-layered mixed forest of beech, spruce and fir (with a low density of Hazel Grouse), there were seasonal changes in habitat selection. In a middle-aged (30-110 years) spruce-dominated forest with birch (with a higher density of grouse), Hazel Grouse stayed in the same habitat throughout the year.

The two first-year siblings, a male and a female, showed different dispersal behaviour. The male, which reached the weight of an adult earlier than its sister, left the family earlier and established a territory earlier than its sister. Dispersal distances were 0.8 km (male) and 6.8 km (female). These data are similar to findings from Sweden.

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Anti-predator behaviour of Black Grouse *Tetrao tetrix* chicks as influenced by hen-rearing versus hand-rearing*

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Introduction

This paper describes experimental studies on the behaviour of captive-reared Black Grouse *Tetrao tetrix* to test the idea that these are particularly vulnerable to predators because anti-predator behaviours are lost in captive birds. High mortality after release is often considered to be due to especially high vulnerability to predators. The question is whether certain rearing conditions cause a change of behaviour which differs from the behaviour of wild Black Grouse.

In one rearing period, the anti-predator behaviour of hand-reared (= artificially reared) and reared by female Black Grouse (= naturally reared) Black Grouse chicks in pens and its development in their first weeks of life were compared (initially with a small sample) and analysed in regard to possible differences in responses of the two chick groups.

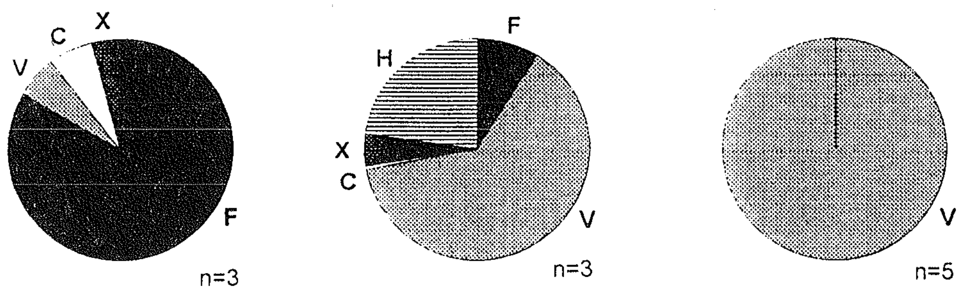
Methods

The trials were carried out with four groups of chicks (two naturally reared with 7 chicks each and two hand-reared with 8 and 9 chicks), in each case at 4, 6, 8 and 10 weeks of age. Due to methodical difficulties, the first three weeks of life were not investigated. Neither female Black Grouse had previously reared a brood. One of these females (3 years old) was hand-reared. The other (1 year old) was reared by a female Black Grouse.

For two days at each age tested, the chicks, together with the female Black Grouse if they were hen-reared, were put in a testing aviary of 18 m^2, fitted with hiding places. To elicit anti-predator behaviour, a live red fox *Vulpes vulpes* was presented at a distance of 40 m. This fox moved across the aviary, on a route which was visible to the grouse along a length of 11 m. The duration of presentation varied between 3 and 116 sec, the distributions of these durations not differing between the groups of chicks (multiple median test). With each group of chicks and within each age class, three identical trials were performed. The behaviour of the chicks in the presence of the fox and during the after-response (that is, continuation of reaction after predator presentation had ended) were recorded.

Results

The trials showed differences in the development of some parameters of anti-predator behaviour between artificially reared and naturally reared Black Grouse chicks. The most common patterns of anti-predator behaviour found during the trials were vigilance, freezing, crouching and hiding in cover. Freezing behaviour (that is, remaining motionless in the previous position) occurred during all kinds of behaviour, e.g. during feeding or vigilance. To develop freezing behaviour, even for artificially reared chicks, an encounter with the fox was not necessary. In supplementary trials, chicks which saw the fox for the first time at the age of 10 weeks showed complete anti-predator behaviour including freezing.

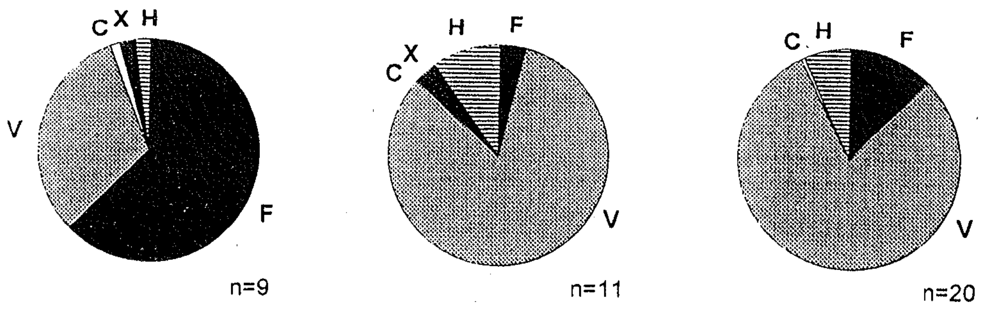


NA
chicks naturally reared
hen artificially reared

NN
chicks naturally reared
hen naturally reared

A
chicks artificially reared

Fig. 1. Arithmetic means of behaviour patterns during fox-presentation in n trials at four weeks of age.
F = Freezing, V = Vigilance, C = Crouching, H = Hiding in cover, X = other kinds of anti-predator behaviour.



NA
chicks **naturally** reared
hen **artificially** reared

NN
chicks **naturally** reared
hen **naturally** reared

A
chicks **artificially** reared

Fig. 2. Arithmetic means of behaviour patterns during fox-presentation in n trials at four to ten weeks of age. Abbreviations see Figure 1.

At four weeks, hen-reared chicks (groups NA, NN) already reacted in a sophisticated way with vigilance, freezing, crouching, hiding in cover and other kinds of anti-predator behaviour, whilst hand-reared chicks (group A) of this age showed only vigilant behaviour (Fig. 1).

Hand-reared chicks showed decreasing proportions of vigilant behaviour with increasing durations of presentation (Spearman rank correlation coefficient $r_s = -0.572$, $P_2 \geq 0.01$, $n = 21$) whilst freezing increased ($r_s = 0.523$, $P_2 \geq 0.05$, $n = 21$). Nevertheless, proportions of freezing behaviour did not increase continuously but began to be shown in durations of presentation above 20 secs. Since no such correlations were found in hen-reared chicks (i.e. the proportion of freezing did not correlate with duration of presentation, because freezing behaviour appeared within the first second of reaction), hand-reared chicks seemed to need a longer duration of the stimulus presentation to react by freezing.

No other differences depending on rearing conditions could be found. The attention directed at the detected predator did not decrease in any group of chicks. This attention was constantly high, right from the start of detection.

In regard to some parameters of anti-predator behaviour, the chicks of the hen-reared hen (group NN) behaved even more similarly to the artificially raised ones (group A) than to the other naturally reared chicks (group NA). The freezing response in the presence of the fox, for example, was significantly higher in the group of chicks with the hand-reared hen than in both the other groups (multiple median test, X^2 tested by Craddock-Flood's approximated empirical X^2 distribution; $K = 9.1$, $\alpha \leq 0.001$, $n = 40$, $FG = 2$) (Fig. 2). In addition, the hand-reared group A showed more freezing behaviour than the hen-reared group NN.

Analysing the after-response led to analogous results (Fig. 3). Again, the groups NN and A showed similar values. Group NA differed significantly from both the other groups.

A possible explanation for the partly different behaviour of the two naturally reared groups of chicks is that characteristics of the Black Grouse females differed. The parental behaviour of the hand-reared hen in the testing aviary was much more restful and more chick-directed than that of the hen-reared hen. This was more nervous and more easily disturbed. It rarely gave contact calls or vocal warning behaviour and virtually lacked typical characteristics of other hens. Therefore, the chicks of the hen-reared hen probably grew up similar to the hand-raised ones.

Independently of rearing conditions, the chicks uttered the aerial predator alarm call (Klaus et al. 1990) in the first trials at four weeks of age, though this call was released inappropriately, in addition to its normal elicitation by raptors, also in the presence of the fox. In all groups of chicks, the terrestrial predator alarm call (Klaus et al. 1990) was given for the first time indiscriminately at ten weeks of age. There were no differences in the behaviour of the chicks following emission of the terrestrial predator alarm call by the hen or following the aerial or the terrestrial predator alarm call of one of the chicks in the presence of the fox.

Whilst the group members possibly orientated themselves by the warning chick, the chicks responded

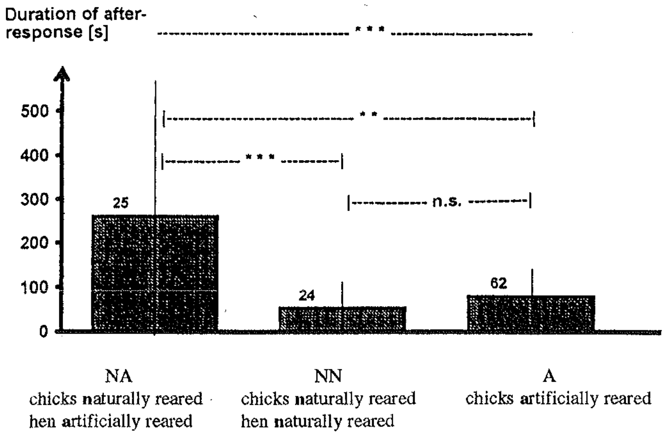


Fig. 3. Duration of after-response. First trial of each group. Analysis of variance ($F = 8.7$; $DF = 2$); assessment of contrasts according to SCHEFF. Significances: **($\alpha < 0.01$); *** = ($\alpha < 0.001$). Figures above bars = numbers of measurements (Chicks evaluated individually).

appropriately to aerial and terrestrial predator alarm calls of the hen even without visual contact with her, that is they looked up and they looked around, respectively.

Discussion

According to Thaler (1987), Hazel Grouse *Bonasa bonasia*, Rock Ptarmigan *Lagopus mutus helveticus* and Rock Partridge *Alectoris graeca* needed continual contact with the hen to keep up initially innate responses to predators (i.e. responses independent of individual experience with predators) throughout development: at the age of six or ten weeks, hand-reared chicks rarely reacted to predators any longer.

By contrast, observations of Brückner (1930) on domestic fowl, Krätzig (1939, 1940) on Hazel Grouse and Black Grouse, Bergmann et al. (1978) on Black Grouse and Scherzinger (1979) on Hazel Grouse suggest a lack of anti-predator behaviour in hand-reared chicks, particularly within the first weeks of life.

Concerning the first three weeks of life in Black Grouse, no statement based on the present study is yet possible, because this period has not been covered so far. A decrease or lack of reaction to a predator corresponding to results of Thaler has not been found in Black Grouse; the hand-reared chicks of age four weeks and older responded similarly to the hen-reared ones (Fig. 2).

From a study on Grey Partridges *Perdix perdix*, Dowell (1988) concluded that the first reaction to a predator is innate but that the duration of a reaction that leads to an effective protection against predators has to be learnt from the parents. Perhaps something similar applies to Black Grouse concerning the start and duration of freezing behaviour in the presence of the predator, because the chicks of the hen with "better" guiding behaviour differed from the other groups of chicks by freezing more often (Fig. 1 and 2).

In this connection, trials with captive Black Grouse which grew up in the wild would be desirable to test whether certain behaviour patterns are essential for Black Grouse, e.g. whether or not freezing is widespread in Black grouse.

Summary

Anti-predator behaviour of two hen-reared and two hand-reared groups of Black Grouse chicks was compared by presenting a live red fox when the chicks were aged 4, 6, 8 and 10 weeks.

Already at four weeks, hen-reared chicks responded with freezing, vigilance and other kinds of anti-predator behaviour when they saw the fox. Hand-reared chicks of this age, on the other hand, showed only vigilant behaviour and first froze at six weeks of age. Moreover, hand-rearing led to a longer minimal duration of fox presentation before the birds reacted by freezing.

However, in regard to vocal warning behaviour, attention to the predator and duration and kind of after-response, no differences were detected due to rearing conditions.

Regardless of rearing condition, the chicks uttered the aerial predator alarm call at four weeks of age, though this call was released inappropriately, in addition to its elicitation by raptors, even in the presence of the fox. In both groups of chicks, the terrestrial predator alarm call was given first at ten weeks of age. Similarly, no differences were found in behaviour of the warned group members both after a terrestrial predator alarm call of the hen and aerial or terrestrial predator alarm calls of a chick in the presence of the fox.

These results are preliminary and experiments need to be continued.

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Variations in clutch defence by incubating female Black Grouse *Tetrao tetrix*

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Clutch losses may significantly reduce the reproductive success of ground-nesting birds (e.g. Lack 1968). For instance, recent studies on grouse (subfamily Tetraoninae) have revealed relatively high and temporally variable nest predation rates (Angelstam 1983, Ellison and Magnani 1985, Bergerud 1988, Myrberget 1988, Lindén 1989, Wegge and Storaas 1990, Willebrand 1992). In some cases, fluctuations in population density may be caused to a large extent by variations in nest loss (Angelstam 1983, Myrberget 1988).

When a grouse clutch is at risk of being depredated, the female is mostly at the nest, because nesting grouse females leave the nest only a few times each day and incubate about 95 % of the time (Erikstad 1986, Klaus et al. 1990). Consequently, the behaviour of the female may be important for the survival of the clutch. Any responses of an incubating female to a predator may be viewed as clutch defence behaviour, and various measures can be used to score the degree of clutch defence (Martin and Horn 1993). In forest habitats with tall shrub cover, however, the distance between the observer, a potential predator, and a female grouse flushing from the nest is usually the only available estimate of clutch defence. It is hereafter called the flushing distance.

Incubating grouse hens generally rely on their cryptic colouring and sit tightly on the nest (Lack 1968, Gabrielsen et al. 1977). This behavioural pattern is apparently adaptive in that the closer the female allows a predator to approach, the higher may be the probability of the clutch to survive. This is due to the possibility that the predator passes by without detecting the female and the nest. In boreal forests, grouse eggs are mostly depredated by mammals and less by birds (Storaas 1988, Willebrand and Marcström 1988), and anecdotal evidence of the behaviour of dogs suggests that mammals hunting primarily by scent may fail to detect a grouse sitting still in the nest (e.g. Hancock 1991). Additionally, hens may avoid exposing their eggs to predators hunting by sight (Erikstad 1986). On the other hand, the risk to the female increases as the predator comes closer, because most of the mammals preying upon eggs (e.g. Storaas 1988) are also capable of killing the female. Thus the flushing distance is a compromise between two conflicting demands, clutch defence and the security of the female, including her likelihood to produce offspring in the future (see Martin and Horn 1993).

Variations in the clutch defence behaviour of grouse are poorly understood, however, in spite of their possible importance for population dynamics (Carlisle 1982). First, few studies have attempted to relate clutch defence to population fluctuation. In a Swedish study area, female Black Grouse *Tetrao tetrix* left the nest more readily in years with low chick production than in years with high production (Angelstam 1983). However, the differences were slight, possibly due to the limited number of observations. In Finland, Pulliainen and Huhtala (1985) reported short flushing distances for incubating female Black Grouse in a peak year of population cycle. Further, clutch defence behaviour may be affected by the "quality" of the female. One may expect an age-related difference in that old hens would show more intense defence (shorter flushing distances), because yearlings lack breeding experience and may have lower body condition (Willebrand 1992). Angelstam (1983) hypothesized that Black Grouse hens in poor condition may invest less in parental care than females in good condition, and that condition may vary between years. Nevertheless, studies on the effects of female age and body condition on clutch defence in grouse are scarce (Myrberget 1970, 1985, Martin and Horn 1993), as well as those relating clutch defence to predation pressure and clutch survival (Martin and Horn 1993).

The aim of this paper is to document variations in the flushing distances of incubating female Black Grouse in study areas where Black Grouse show 6-7 year cycles of high amplitude, typical of the species over most of Finland (Lindén 1988). I compare flushing distances between age classes and between years, and relate them to female body condition, the population density of potentially most important egg predators, and clutch survival.

Study areas

The fieldwork was done in a boreal forest landscape in central Finland in 1989-93. In 1989, female Black Grouse were radio-marked at three sites: at Raatosuo (64 01'N, 27 22'E) in Kajaani, eastern central Finland, and in Tyrnävä (64 44'N, 25 47'E) and in Ylivieska (63 59'N, 24 36'E), western Finland. The study areas were 100-140 km apart. In 1990-93, birds were marked only in the Kajaani study area, at Raatosuo and at Hämeensalmi (64 04'N, 27 21'E) each year, at Tavisuo (63 58'N, 27 25'E) in 1991 and 1992, and at Koukosuo (64 05'N, 27 33'E) in 1992 and 1993. These sites were 5-10 km apart. The number of marking sites each year depended on the number of radio-tags available and the number of females visiting each site.

In 1989, the birds were tracked within 10-15 km from the marking site in each study area. In 1990-93, with improved searching technique (see below), the study area covered 1000-1500 km^2. The terrain in the Kajaani study area was hilly or slightly undulating (125-350 m above sea level). The major habitat types were forests, bogs, clearcuts and plantations. Forests were dominated by Scots pine *Pinus sylvestris* (75 %), interspersed with Norway spruce *Picea abies* and deciduous trees, mostly birches *Betula pubescens* and *B. pendula*. The proportion of bogs in the forestry land area was 44 %, and more than 60 % of the bogs were drained for forestry (Aarne 1993). The field layer was dominated by bilberry *Vaccinium myrtillus* and lingenberry *V. vitis-idaea* in forests, and by bog whortleberry *V. uliginosum* and Labrador tea *Ledum palustre* on bogs.

In the other study areas, Tyrnävä and Ylivieska, the terrain was rather flat, elevated 20-60 and 75-125 m ASL., respectively. Birches were more abundant than in Kajaani, and the area of bogs was higher (Aarne 1993), but otherwise the study areas were rather similar.

Material and methods

Capturing and radio-tagging

Females were radio-marked at a winter feeding station installed on an open bog and supplied with oats at each study site. They were captured in wire-netting traps baited with oats during mid February to early April when they lived in winter flocks with males. Winter feeding was a game management effort carried out by hunters in southern and central Finland. Feeding stations effectively attracted individual Black Grouse within 2-3 km (Valkeajärvi and Ijäs 1989), but unlike some other birds, Black Grouse remained shy and also fed on their natural winter foods (Marjakangas 1992). For these reasons, I feel that Black Grouse captured at feeding stations constitute a representative sample of the local population.

The birds were weighed to the nearest 5 g with a spring balance and their wing lengths measured in mm with the wing flattened and straightened. They were classified as yearlings (hatched the previous season) or adults (2+ years) according to Helminen (1963), ringed with a numbered aluminium leg band and fitted with a 17 g necklace radio transmitter with an expected lifetime of 6-10 months. According to Marcström et al. (1989), necklace radio-tags, 2-3 % of body weight, are preferable to backpacks for gallinaceous birds. In my study, the weight of the tag was 1.6-2.2 % of body weight, and the tag was normally hidden among feathers. The only observable effect of the tag was that I sometimes heard the antenna slapping against wings when a radio-marked bird was flying. However, tags may not have affected the flushing distances of radio-marked females, because they were similar to those of unmarked incubating Black Grouse hens flushed by chance (N = 5).

Tracking and data composition

The birds were located by triangulation using portable receivers and hand-held and vehicle-mounted 4-element yagi-antennas. The disappearance of many females during breeding dispersal in April resulted in considerable loss of data in 1989, because tracking was restricted within 10-15 km around the marking sites. In 1990-93, missing females were sought by aircraft over an area of 60 x 60 km, and were mostly found at a distance of 20-35 km from the marking site (Marjakangas et al. 1991).

To maximize the number of nests found, an attempt was made at visiting nests as early as possible during incubation. Therefore the females were flushed when expected to have initiated incubation. The nest site was approached at a steady pace, and the distance between the observer and the nest was measured at the moment the female flushed. The eggs were counted and numbered, and usually two eggs were tested in water to determine the stage of incubation (Westerskov 1950). In some cases when the clutch appeared to be incomplete, the flushing distance measured at the next visit to the completed clutch was accepted, because flushing distances were longer during laying than during incubation period (Marjakangas unpubl.). However, if the female had layed only one more egg, the flushing distance at the first visit was accepted, because female Black Grouse probably start to incubate between laying of the last two eggs (Klaus et al. 1990).

The females were flushed mostly during 0700-1800 hours. The flushing distance may be affected by whether the female is just about to take a break, or has just arrived at the nest. The possible effect of the incubation rhythm was not controlled, but as females take only a few recesses a day (Klaus et al. 1990), this potential source of error may be negligible.

The presence of the female at the nest was checked by triangulation once or twice a week, and mostly two more visits were made at the nest to observe clutch fate. A clutch loss refers here to the total loss of a clutch, while a partial loss was ignored except when the female as a result abandoned the reduced clutch. The clutches of ten females killed during incubation, one clutch destroyed by man, and one abandoned for an unknown reason were excluded from clutch survival analysis. Potential egg predators present in the study areas were red fox *Vulpes vulpes*, raccoon dog *Nyctereutes procyonoides*, pine marten *Martes martes*, badger *Meles meles*, mink *Mustela vison*, stoat *M. erminea*, least weasel *M. nivalis*, brown bear *Ursus arctos*, red squirrel *Sciurus vulgaris*, Raven *Corvus corax*, Hooded Crow *C. corone*, Jay *Garrulus glandarius* and Magpie *Pica pica*.

The dates of the commencement of incubation were determined directly, by egg flotation (accurate for the first 8 days of incubation) and backdating, or by backdating from hatching dates, assuming an incubation period of 25 days (Klaus et al. 1990). The median date for initiating incubation of the first clutch was 20 May (Marjakangas unpubl.). Only the flushing distances at the first visits at first nests during incubation are involved here, because the level of clutch defence may be different in birds at first nests and renests, and for different stages of incubation (Martin and Horn 1993).

Data analyses

The yearlings weighed less than the adults (mean weights 967.9 and 923.9 g, respectively; t-test, $t = 8.18$, $df = 168$, $p = 0.0001$) and had shorter wings (234.8 and 238.3 mm; Mann-Whitney U-test, $z = 4.78$, $N = 168$, $p < 0.001$). Thus the age classes were treated separately when adjusting body weight for wing length, which provides a good estimate of structural size (Robb et al. 1992). There appeared to be a relationship between weight and wing length, and the best fit was achieved using a linear regression model, $y = 4.045x - 81.933$

Table 1. Flushing distances (m) of incubating female Black Grouse in 1989-93.

	Yearlings			Adults		
Year	Median	Range	N	Median	Range	N
1989	2.2	0.5-9.5	6	2.5	1.0-4.0	8
1990	2.0	1.0-6.0	17	2.0	0.5-10.0	25
1991	3.0	0.2-6.0	13	2.5	0.3-7.0	33
1992	2.0	0.3-6.0	21	1.5	0.2-7.0	21
1993	2.5	0.8-5.0	13	1.5	0.5-4.0	13

Table 2. Track-indices (tracks/10km/24 h) of red fox and pine marten in the Kajaani study area, according to wildlife triangle indices in winter 1989-93.

Year	Red fox	Pine marten
1989	4.3	0.3
1990	5.2	0.4
1991	3.7	0.1
1992	3.5	0.5
1993	3.1	0.6

($t = 3.67$, $p = 0.0005$) for yearlings, and $y = 2.299x + 376.772$ ($t = 2.28$, $p = 0.025$) for adults (y = weight, x = wing length). The weight of each bird was adjusted by adding the residual (positive, negative or zero) of the regression to the overall mean value for each age class (Martin and Horn 1993). This adjusted weight is hereafter called body condition.

Non-parametric tests were used in most comparisons because of the non-normality of data sets, and the probability level of 0.05 was considered significant. Differences in flushing distances between study areas and years were tested using Kruskal-Wallis test. A two-tailed Mann-Whitney U-test was used to test differences between two independent data sets and in paired comparisons after Kruskal-Wallis test. In the latter case, the level of rejection of a null hypothesis was obtained by dividing 0.05 by the number of comparisons made (Dixon et al. 1985). Differences in clutch losses between years were tested with X^2-test. A relationship between two variables was examined using Pearson's product moment correlation or Spearman rank correlation.

Ten birds were tracked during two different years and hence they contributed two values for some analyses. However, excluding their second values did not affect the results, and therefore all values are included. A two-tailed paired t-test was used to compare their flushing distances between years.

Black Grouse and predator densities

In Finland, grouse are counted in August and the tracks of mammals in winter in permanent wildlife triangles (Linden et al. 1989). The results of these counts for the Kajaani study area were obtained from the Game Division of Finnish Game and Fisheries Research Institute. The densities were compared with the Raatosuo site as the central point, using the data from the triangles within 10 km with full impact and those from the triangles 10-50 km apart with impact decreasing linearly from 1 to 0. The number of triangles included was 19-43. The track-counts are assumed to give good indices of predator densities.

Results

Altogether, 170 females were flushed from their first nests. The flushing distances did not differ between the study areas in 1989 ($H = 0.79$, $df = 2$, $p < 0.75$), and so the data were pooled.

There was a weak negative correlation between the flushing distance and the day from the start of incubation ($r = -0.26$, $N = 167$, $p < 0.01$; Marjakangas, unpubl.). However, only a few nests were found during later stages of incubation (median day for the first visit at the nest = day 4).

Variations between age classes and years

The flushing distances ranged between 0-10 m and showed a skewed distribution (Fig. 1). They did not differ between the age classes ($z = -0.62$, $p > 0.5$). The females tended to flush at a greater distance in 1991 than in other years (Table 1), but the differences were not significant ($H = 7.44$, $df = 4$, $p < 0.5$). However, the between-year variation was slightly different for the age classes (yearlings: $H = 3.60$, $df = 4$, $p < 0.5$, $N = 70$; adults: $H = 8.50$, $df = 4$, $p < 0.1$, $N = 100$). The flushing distances of the adults differed between 1991 and 1992 ($z = -2.27$, $p < 0.05$) and between 1991 and 1993 ($z = -2.53$, $p < 0.05$).

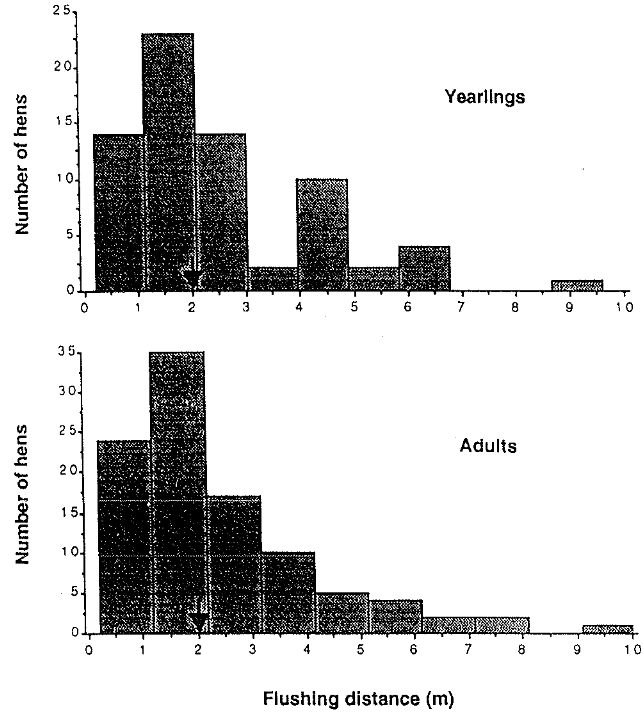

Fig. 1. Distribution of the flushing distances of incubating yearling and adult female Black Grouse in 1989-93 (years combined). Arrows denote medians.

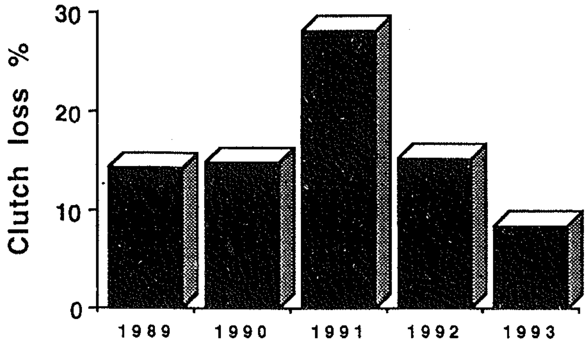

Fig. 2. Proportion of Black Grouse clutches predated during incubation.

The ten individuals tracked during two breeding seasons flushed at different distances in different years ($t = -3.14$, $df = 9$, $p = 0.012$). For seven females in which the other year was 1991, the mean distance was 3.6 m in 1991 and 1.7 m in 1990, 1992 and 1993 ($t = 2.70$, $df = 6$, $p = 0.036$).

Relationship to body condition and clutch survival

In yearlings and adults, there was no significant relationship between flushing distance and body condition ($r = 0.157$, $df = 96$, $p > 0.1$, and $r = -0.108$, $df = 68$, $p > 0.1$, respectively). Clutch losses during incubation varied, but not significantly, between years, being relatively highest in 1991 ($X^2 = 4.93$, $df = 4$, $p = 0.295$; Fig. 2). The flushing distances were slightly different according to whether the clutch survived (median = 2.0 m, $N = 129$) or was predated (median = 1.5, $N = 27$)($z = -1.77$, $p < 0.1$). The distances were similar in 1991, however, when 28 clutches survived and 11 were predated ($z = -0.05$, $p > 0.9$). They were similar according to clutch survival for both age classes.

Black Grouse and predator densities

The Black Grouse autumn population showed a cyclic peak in Kajaani (and in the other study areas) in 1989, crashed in 1990 and 1991 to about one fifth of the density in 1989, and then started to increase (Fig. 3). Parameters of the breeding success, e. g. the proportion of females with broods and average brood size were at lowest in 1991.

The red fox and the pine marten were important predators probably on both grouse eggs and chicks (Marcström et al. 1988). Table 2 shows that the track-indices of pine martens were at lowest in 1991 and that those of red foxes fluctuated relatively less, with the most pronounced change between 1990 and 1991.

Discussion

Differences between age classes

Yearling females may be inferior to adult ones in various performances of breeding (e.g. Willebrand 1988, 1992), but I found no overall difference in the flushing distances of yearling and adult female Black Grouse. Thus the level of clutch defence was probably independent of female age, even though yearlings lack breeding experience and have lower body condition than adults (Willebrand 1992, Marjakangas unpubl.). Myrberget (1970, 1985) and Martin and Horn (1993) nevertheless showed a lower level of clutch defence in yearling than in adult Willow Ptarmigan *Lagopus lagopus* females. According to Martin and Horn (1993), a likely explanation for this difference is that the number of recruits per nest increases with the age class of the pair (Hannon and Smith 1984). Willebrand (1992) reported a tenfold difference in the breeding success of female Black Grouse in favour of adults, whereas no difference between age classes was found in the present study areas (Marjakangas unpubl.). Thus the likelihood of producing recruits might have been quite similar for both age classes, and this might explain why there was no age-related difference in clutch defence.

Although the overall differences in flushing distances among years were slight, examination of the age classes separately revealed that the distances of adults were greater in 1991. Yearlings also tended to flush at greater distances in 1991, but the differences were more obscure possibly because of the large variation between females. Observations on the same females in different years provided a more compact data set, and they confirmed that females really showed lower clutch defence in 1991 than in the other years. These observations and the fact that both yearlings and adults tended to flush at greater distances in 1991 point to some extrinsic factor(s) as the proximate cause of differences between years, rather than to intrinsic differences in behaviour between cohorts (e.g. Theberge and Bendell 1980).

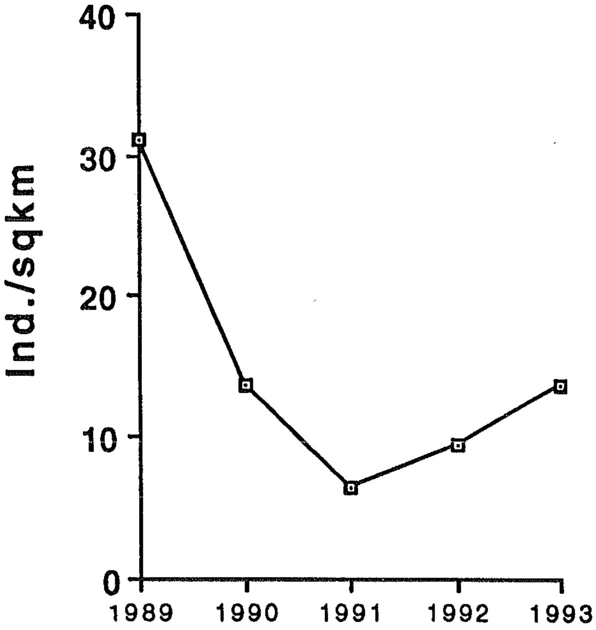

Fig. 3. Fluctuations in Black Grouse density (adults and juveniles combined) in the Kajaani study area according to wildlife triangle indices in August 1989-93.

Body condition

In some birds the intensity of clutch defence varies with body condition (e.g. Myrberget 1985, Hogstad 1993, Martin and Horn 1993), but this study failed to find such a relationship within the age classes. Opposite to what might have been expected, the females showed higher condition in 1991 than in any other year (Marjakangas unpubl.). Body condition was measured here 1.5-3 months prior to the commencement of incubation. Grouse females mostly maintain their body condition at the same level relative to their conspecifics between consecutive years (Robb et al. 1992, Marjakangas unpubl.) ,and this probably applies to consecutive seasons as well. However, body condition measured in late winter may not be suitable to study differences relative to breeding performance between years, because the level of females' nutrient reserves collected for reproduction in spring may vary among years (e.g. Siivonen 1957, Willebrand 1988).

The availability of spring food for grouse females in the north depends on two factors: melting of snow, which in turn depends on spring temperatures (Siivonen 1957), and fluctuations in plant production (e.g. Angelstam 1983, Pulliainen and Tunkkari 1991). Spring was very early in Kajaani in 1991, and females had access to field layer plants for several weeks before laying. However, they began breeding at the normal time and laid relatively small clutches (Marjakangas unpubl.), and clutch size may correlate with condition (e.g. Willebrand 1988). Thus the females' body condition may really have been poor in 1991 possibly due to low production of important food plants, resulting in small clutches and low level of clutch defence, as proposed by Angelstam (1983). Hens in poor condition may be less able to avoid capture than those in good condition (Martin and Horn 1993), and thus sit less tightly on the nest. Eggs laid by females in poor condition may also be less viable and therefore less valuable than those laid by hens in good condition (Moss and Watson 1984, Steen et al. 1988). However, the survival of chicks hatched in 1991 was only slightly lower than the mean survival for 1989-93 (Marjakangas unpubl.).

Flushing distance and clutch survival

Comparison of flushing distances with clutch survival and predator abundance yielded partly confusing results. As in Willow Ptarmigan (Myrberget 1985, Martin and Horn 1993), the level of clutch defence did not differ significantly according to whether the clutch was later depredated or not. I cannot find a reasonable explanation why the females with clutches predated later tended to flush at shorter distances.

Though there may not be any causal relationship between the level of clutch defence and clutch survival, the results nevertheless suggest that they may vary in parallel. One may expect that females would show less clutch defence in a year with high predation risk. However, clutch losses were highest and flushing distances relatively long in 1991, even though the abundance of red foxes and pine martens was relatively low in the preceding winter. One possible explanation for this discrepancy is that these predators might have been more abundant in the study area in spring than in winter 1991 due to strong immigration. Second, some other predator species may have contributed to clutch losses relatively more in 1991. One peculiar feature in spring 1991 was that several females were killed by some small mammalian predators, possibly stoats (Marjakangas unpubl.). Stoats may also prey upon grouse eggs (Myrberget 1985). Third, clutch defence and survival may have been affected by a functional response from egg predators in 1991. If the general food situation is poor, predators should be more active in searching, and hence the frequency of encounters with predators might have been relatively high in 1991.

There is also a potential explanation combining body condition and predation. Avian egg predators apparently locate grouse nests by watching females moving to and from their nests (Erikstad et al. 1982). Females in poor condition leave the nest much more frequently than those in good condition (Erikstad 1986), and therefore their clutches may be more vulnerable to predation by corvids. If female Black Grouse were in relatively poor condition in spring 1991, as suggested by their low average clutch size, they may have lost many clutches to corvids.

Conclusion

Late winter body condition and predator abundance, as measured in the study, did not explain variation in flushing distances. Nor did I find a relationship between clutch survival and flushing distances. Relatively long distances and high clutch losses in 1991 are likely to have a common cause, but flushing distances were possibly too variable to affect clutch survival.

The main aim here was to study whether important between-year variation existed in clutch defence by female Black Grouse. They indeed showed less clutch defence and thereby risked less their own security in one year characterized by poor chick production. This is in accordance with the prediction of Carlisle (1982) that animals in a cyclic population should provide less parental care when environmental conditions deteriorate. Variation in clutch defence among years was here due to extrinsic factors, possibly involving spring food availability, predation risk or both. Then why did the females not show greater flushing distances also in 1990, when chick production was also rather low and the population crashed? Possibly environmental conditions were favourable during nesting but less favourable during the brood period. Thus the relative importance of parental care may differ between incubation and brood period, and variations in brood defence should be included in future studies on the population dynamics of Black Grouse.

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Summary

The distances from the observer at which incubating radio-equipped Black Grouse females flushed from nests were studied in central Finland in 1989-93. There was no overall difference between yearlings and adults. Flushing distances tended to be greater in 1991, and those of the females monitored during two different seasons were strikingly longer in 1991 than in other years, suggesting that females provided less clutch defence in 1991 due to extinsic factors. Flushing distances were not correlated with body condition measured 1.5-3 months before breeding. However, year 1991 was characterized by relatively small clutches and poor chick production, and thus females probably had poor breeding condition, possibly due to a low availability of nutritious food. Clutch losses were higher in 1991 than in other years, but flushing distances did not differ significantly according to the later fate of clutches, and they were not related to the abundance of the red fox and the pine marten. Thus, the lower level of clutch defence in 1991 may be explained by poor breeding condition, or alternatively, by functional response from foxes and martens, or by the impact of other predators.

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Habitat evaluation and management

The importance of large herbivore management to woodland grouse and their habitats

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Introduction

Over the last 100 years, numbers of Black Grouse *Tetrao tetrix* have declined over much of their European range (reviewed in Cramp and Simmons 1980). In upland Britain, large-scale losses of suitable habitat on moorland edges, caused principally by either agricultural expansion and intensification or by afforestation, are associated with this decline (Cramp and Simmons 1980). On remaining moorland, a combination of increased numbers of sheep, particularly in northern England (Anderson and Yalden 1981), and a doubling of red deer *Cervus elaphus* numbers in many parts of Scotland (Fig. 1) (Callander and MacKenzie 1991) have been associated over the last 40 years with extensive deteriorations in habitat quality.

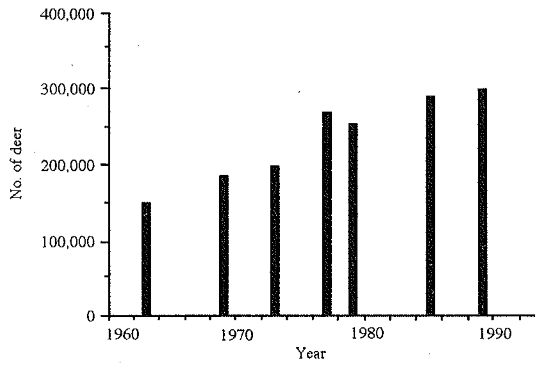

Fig. 1. Increases in the numbers of wild red deer in Scotland since 1960.

Source: Red Deer Commission (1989).

There have been similar losses in the extent of native woodland in upland Britain. The extent of native birch *Betula* spp. woodland and pine *Pinus sylvestris* forest, favoured by both Black Grouse and Capercaillie *Tetrao urogallus*, has decreased (O'Sullivan 1977, Bain 1987). Remnant pine forests are highly fragmented and tend to be small, with only four of the 35 principal woods remaining being larger than 10 km^2 (Steven and Carlisle 1959).

The availability of sheltered grazings in winter is important for red deer and large numbers can be found in pinewoods (Callander and MacKenzie 1991). Many woods are heavily grazed and there is considerable concern that high deer numbers have prevented regeneration for more than 200 years in some forests (Watson 1983). Several studies have considered the effects of red deer on the ability of Scots pine to regenerate (Holloway 1967, Watson 1983), but the effects of grazing on the field layer communities have been relatively little studied. Bilberry *Vaccinium myrtillus,* one of the dominant species of the forest floor, is an important food plant for both Capercaillie (Rolstad and Wegge 1987, Storch 1995) and Black Grouse (Picozzi and Hepburn 1984). Buds are eaten in spring, berries and leaves in late summer and shoots in winter. In addition, bilberry supports high densities of lepidopteran larvae (Baines et al. 1994) which are preferred food of chicks (Kastdalen and Wegge 1984).

Black Grouse prefer tall vegetation (Parr and Watson 1988), but in many places the ground vegetation on favoured lower moorland and woodland edge has been grazed very short and preferred plant species have been reduced (Baines et al. 1944). This study investigates the importance of habitat quality associated with differences in grazing intensity on the density and breeding success of Black Grouse in moorland and pine forest habitats in northern Britain.

Methods

Study areas

Moorland sites Five blocks of moorland, one each in the North Pennines, the Borders, Central Perthshire, North Perthshire and Inverness-shire were studied in 1991 and 1992. Each block contained two matched pairs of moors differing in grazing intensity by either sheep or red deer. Lightly grazed moors had relatively low sheep densities with grazing largely confined to summer. Included in this definition were partly afforested moors, where both sheep and deer had been excluded from recently planted forests (Table 1). An additional classifying criterion was the presence of regenerating scrub, usually birch or willow *Salix* spp. Within moorland blocks, most paired moors differing in grazing treatment were adjacent to each other to minimise differences due to climate, geology or geomorphology.

Pinewood sites Eight forests lying on a broad east to west transect across the Scottish Highlands were studied (Fig. 2). To assess the effects of grazing on the forest floor vegetation and its associated arthropod fauna, three matched pairs of sample plots subjected to differing grazing pressures were compared in each of the eight forests. Different grazing intensities were usually found where deer exclosures had been erected to allow tree regeneration, but also occurred across boundary fences between sections of forest of different ownership.

Vegetation and invertebrates

Sweep netting was used to measure the relative abundance of invertebrates. On each moor, samples were taken at 25 points 150m apart on two 1 km transects across the centre of areas where numbers of Black Grouse were counted (see below). At each sample point, 25 sweeps of the vegetation were made using a net of 0.45m diameter. Invertebrates caught were sorted into main groups. In each of the eight forests, 125 sweeps (5 x 25) of vegetation dominated by bilberry were made on the three matched pairs of plots.

The efficiency of sweep netting may be biased by grazing which affects vegetation length and structure (Southwood 1978). To test for this, densities of larvae were estimated in a 900cm^2 quadrat of bilberry by hand searching adjacent to each of the swept areas. Significant positive relationships were found between the numbers of larvae found by hand searching and the numbers caught by sweep netting in both grazed and ungrazed forests. The slopes of the regressions did not differ between treatments (ANCOVA: $F_{1,45} = 1.58$, NS), and from this it was assumed that sweep netting provided an unbiased estimate of larval abundance over the range of different vegetation lengths and structures irrespective of grazing. Consequently, all data on invertebrates given below are from sweep netting.

Vegetation on the moorland sites was classified as heather *Calluna vulgaris* and *Erica* spp., other woody shrubs, grass, rushes *Juncus* spp., cotton grass *Eriophorum* spp. and "others". Forest vegetation was categorised as bilberry, heather, grass or moss. The proportion of each in a 10m x 1m quadrat encompassing the sweep net line was estimated to the nearest five per cent. Halfway along the line, the height of the vegetation was measured. In forests, all aerial stems and foliage of bilberry within a 900 cm^2 quadrat were collected and weighed when fresh.

Densities of male Black Grouse

Counts of male Black Grouse displaying on traditional arenas or leks were made at or just after dawn between mid April and mid May on all 20 moors. Counts were also done in four of the forests, two where red deer numbers have been reduced and two where they remain high. Numbers of males at each lek were usually counted at least twice and the maximum numbers recorded. Numbers of males at leks were transformed into density estimates using the area of ground lying between 220-465m in Scottish study areas and 340-590m in England. These altitudes encompassed 95% of leks in Scotland (n=387) and all leks in England (n=49) found in a survey of 37 10km grid squares (Baines unpubl.).

Black Grouse breeding success and female densities

Searches for broods using pointing dogs were made at all 20 moors in late July and August and in four of the forests. The aim was to find a minimum of 10 females at each site from which to estimate breeding success. Consequently, the size of areas searched varied in relation to breeding density and ranged from 1.5 to 6.0 km^2, with a mean of 3km^2. It was assumed that females without broods had attempted to breed, but had failed. The total number of females flushed at each site was used to calculate female density. Searches for broods

Table 1. Size, land-use and management of the 20 study moors. Gr = grouse moor, Sh = sheep farm, For = forestry, Deer = red deer forest.

Moor	Size of study area (km^2)	Main land use	Sheep density	Winter sheep grazing	No. of red deer shot/annum	Grazing type
North Pennines	121	Gr	5000	No	0	Low
	8	Gr	1200	No	0	Low
	126	Gr	13000	Yes	0	High
	7	Sh/Gr	1000	Yes	0	High
Borders	60	For/Gr	0	No	0	Low
	19	For/Gr	0	No	0	Low
	13	Gr/Sh	2000	Yes	0	High
	77	Gr/Sh	8000	Yes	0	High
Central Perthshire	14	For/Gr	1000	No	35	Low
	10	Deer/Gr	750	Some	25	Low
	6	Deer/Gr	750	Yes	25	High
	14	For/Sh	1000	Yes	140	High
North Perthshire	57	Deer/Gr	1800	No	100	Low
	30	For/Sh	900	No	50	Low
	81	Deer/Gr	1000	No	120	High
	15	Sh	1050	Yes	20	High
Inverness-shire	100	Deer	0	No	250	Low
	85	Deer	0	No	50	Low
	121	Deer/Gr	0	No	300	High
	45	Deer/Gr	1000	Yes	50	High

were also made at two moors in June just after hatching to assess habitat selection by young broods. Estimates of densities of female Capercaillie were made in each of the eight forests either whilst counting Black Grouse or from Moss (1986) or Picozzi et al. (1992).

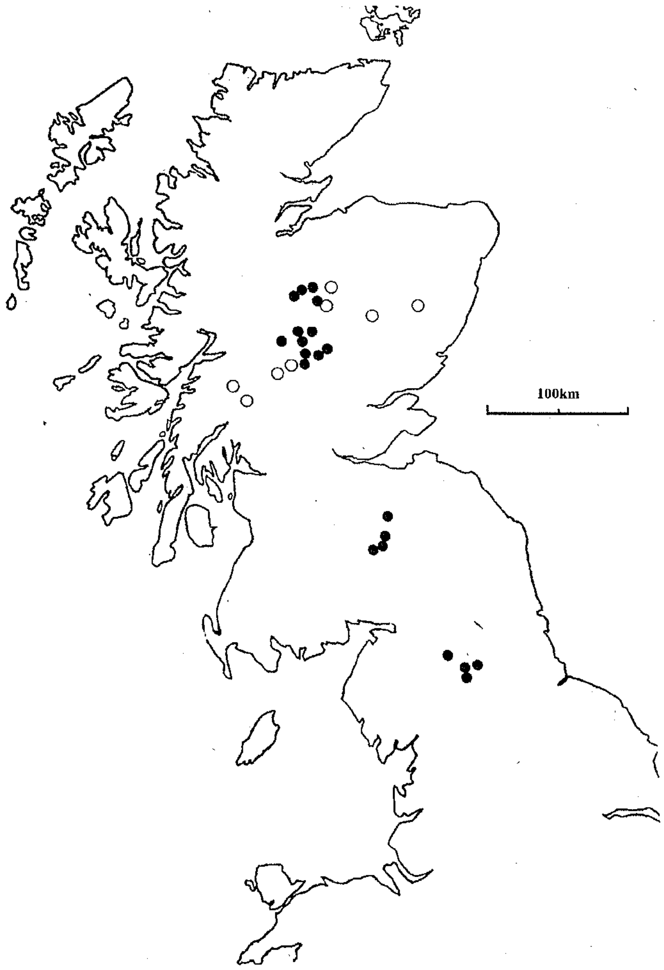

Fig. 2. Location of the 20 moorland study areas (filled circles) and 8 native pine forest study areas (open circles).

Analysis

Densities of male and female Black Grouse, breeding success, vegetation height and invertebrate abundance were calculated for each moor. Differences in parameter means between the two grazing treatments and between regions were analysed by two-way blocked ANOVA. Data on breeding success were only included if five or more females were found on a moor. Fewer than five females were considered to give an unreliable estimate of breeding success.

Vegetation compositions from all samples were summed for each moor and expressed as mean proportions. When summed, the proportion equalled one and hence the initial data could not be considered independent of each other. Data were made independent by calculating the ratios of one proportion over the others using one group as the denominator. The results of the analysis do not depend on which group was used as the denominator. The ratios were then log transformed to normalise the data. The analysis of differences in the composition of the ground vegetation was carried out by multi-variate analysis of variance (MANOVA) applied to the log ratios (Aitchison 1986).

Differences in bilberry biomass and height between grazing treatments were analysed by one-way ANOVA. Invertebrate abundance was sampled in two years at the same forest plots, thus representing a repeated measures design which was analysed using MANOVA on log (x+1) transformed data. A step-wise multiple regression analysis was used to identify factors explaining significant amounts of variation in the abundance of lepidopteran larvae on bilberry. All analyses were performed using SYSTAT Version 5.0 (Wilkinson 1990).

Results

Vegetation

Heavily grazed moors tended to be dominated by grasses and rushes and had less heather than equivalent lightly grazed moors, but differences measured were not significant. Grazing did however reduce the height of vegetation by an average of 32% ($P<0.001$) (Table 2). Similarly, grazed areas in forests had significantly more grass ($P<0.05$) and significantly less heather ($P<0.01$) (Table 3). Although

Table 2. Regional differences in mean vegetation height (cm) between ten lightly grazed and ten heavily grazed moors. Means are from 25 samples on each of two moors (n=50).

	Region				
	Pennines Mean±S.E.	Borders Mean±S.E.	C.Perth. Mean±S.E.	N.Perth. Mean±S.E.	Speyside Mean±S.E.
Lightly Grazed	16.5±0.5	27.3±3.0	28.5±1.5	34.3±1.8	25.0±2.0
Heavily Grazed	15.0±1.3	23.5±3.5	17.8±2.5	19.5±2.3	14.3±0.5
% diff.	9%	14%	38%	43%	43%

ANOVA: Effect of Region: $F_{4,10} = 9.78, P<0.01$
Effect of Grazing: $F_{1,10} = 42.36, P<0.001$

Table 3. Vegetation composition of the field layer and the primary production of bilberry in eight pinewoods in the Scottish Highlands. Data presented are the means ± one standard error of the forest means. Heather = *Calluna* and *Erica* spp., Grass = grass and moss.

	Ungrazed Mean ± S.E.	Grazed Mean ± S.E.	"F" (df 1,39)	Sig.
% Heather	36 ± 6	20 ± 6	12.41	$p<0.01$
% Grass	11 ± 7	24 ± 7	15.23	$p<0.05$
% Bilberry	47 ± 3	52 ± 5	1.81	ns
Bilberry height (cm)	25 ± 2	13 ± 1	146.20	$p<0.001$
Bilberry biomass (kg/m2)	1.6 ± 0.1	0.7 ± 0.1	83.09	$p<0.001$

Table 4. Geometric mean numbers of invertebrates caught per 25 sweeps on 10 lightly grazed and 10 heavily grazed moors and on bilberry in grazing exclosures and grazed areas of eight native pine forests.

	Moorland			Forest		
Group	Light Mean	Heavy Mean	Sig.	Light Mean	Heavy Mean	Sig.
Coleoptera	4.1	2.6	ns	9.1	5.0	$p<0.01$
Hemiptera	7.2	3.6	$p<0.05$	3.6	3.5	ns
Diptera	7.7	7.9	ns	18.4	10.1	$p<0.001$
Araneae	4.3	1.9	$p<0.01$	13.4	6.6	$p<0.001$
Lepidoptera (larvae)	3.1	0.7	$p<0.01$	161.0	46.0	$p<0.001$
Hymenoptera	1.9	0.9	ns	20.2	7.3	$p<0.001$
Symphyta (larvae)	0.6	0.6	ns	0	0	ns
Total	34.4	20.9	$p<0.01$	230	80	$p<0.001$

grazing did not affect the amount of ground covered by bilberry, it had significant effects on its height and biomass. In grazed forest, bilberry was, on average, only half the height ($P<0.001$) and had an above ground biomass of less than half that in ungrazed exclosures ($p<0.001$).

Invertebrates

Overall, 41% fewer invertebrates were caught on heavily grazed than on lightly grazed moors ($p<0.01$) (Table 4). This was largely attributable to 77% fewer lepidopteran larvae ($p<0.01$), 56% fewer spiders and harvestmen (Araneae) ($p<0.01$), 50% fewer plant bugs (Hemiptera) ($p<0.05$) and 70% fewer Hymenoptera ($p>0.1$,ns) caught on heavily grazed moors. Numbers of flies (Diptera) and sawfly (Symphyta) larvae did not differ significantly between grazing treatments.

In pine forests, almost three times fewer invertebrates were caught in deer-grazed forest than were caught in adjacent deer exclosures ($p<0.001$). Numbers of lepidopteran larvae caught were four-fold fewer, whilst Hymenoptera, chiefly wood ants *Formica rufa* were three-fold fewer and beetles (Coleoptera) ($p<0.01$), spiders and harvestmen ($p<0.001$) and flies ($p<0.001$) all half the numbers caught in ungrazed exclosures.

Numbers of lepidopteran larvae caught differed between forests, with bilberry stands in the eastern Highlands supporting, on average, more than seven times more larvae than bilberry stands in forests in the western Highlands (Fig. 3). Overall, 83% of the variation in the numbers of larvae caught on bilberry at each site within the forests was attributable to four factors. These were grazing intensity, i.e. bilberry biomass ($r^2 = 0.53$) and the proportion of bilberry tips that were grazed ($r^2 = 0.37$), together with mean annual rainfall ($r^2 = 0.29$), altitude ($r^2 = 0.13$) and tree density ($r^2 = 0.15$) (Table 5).

Grouse densities

Moors with low grazing pressures supported densities of male Black Grouse 35-40% higher than equivalent moors with high grazing pressures ($p<0.05$)(Table 6). Densities of females were almost twice as high on lightly grazed moors than on heavily grazed moors, with an average of 3.3 females km^{-2} compared to 1.8 ($p<0.05$). The two forests where deer numbers had been reduced supported similar densities of males, but tended to have more females than the two forests where deer numbers remained high. This tendency was supported by counts of females inside and outside grazing exclosures in one of the heavily grazed forests, with population densities of females inside exclosures (3.1 km^{-2}) over twice that outside these exclosures (1.4 km^{-2}).

Densities of female Capercaillie were positively correlated with larval abundance along the west to east transect (Spearman rank $r_s = 0.9$, n=8, $p<0.01$). Highest densities were found in eastern forests with up to 4.5 females km^{-2}. Capercaillie were absent from three of the four western forests sampled, having become extinct in two in the 1980s and having declined to virtually zero in the fourth (Fig. 3).

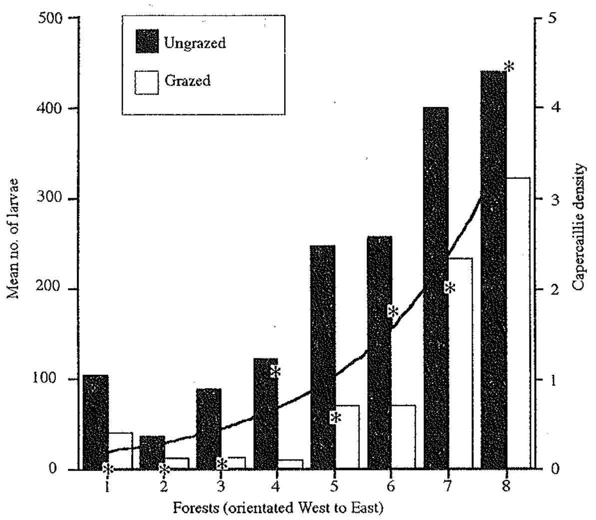

Fig. 3. Mean number of lepidopteran larvae per 25 sweeps in grazed and ungrazed areas of each of eight native pine forests. Forests are numbered from one to eight in relation to their position along a west (1) to east (8) transect. Summer densities of Capercaillie (females km^{-2}) are superimposed (asterisks).

Source: Data from Baines (unpubl.), Moss 1986 and estimated from Picozzi et al. 1992.

Breeding success

On moorland, breeding success was better where grazing was light, 60% higher in 1991 and 25% in 1992 (both $p<0.02$) (Table 7). In 1991, higher breeding success on lightly grazed moors was largely due to 42% higher mean brood sizes ($p<0.05$). In 1992, the difference in mean brood size between grazing treatments was only 8%, but lightly grazed moors had, on average, 17% more females with broods ($p<0.05$).

Brood habitat selection

A comparison of vegetation height and invertebrate numbers at brood locations and at random locations showed that chicks selected taller vegetation ($p<0.01$) where there were more invertebrates (Perthshire $p<0.001$, Pennines $p<0.05$) (Table 8). The sites where broods were found contained almost twice as many beetles and plant bugs and up to three times more Hymenoptera and larvae (Lepidoptera only) as were found at random sites.

Discussion

Densities and breeding success of Black Grouse were highest in areas where numbers of large herbivores were reduced. There could be at least three different causes. First, high levels of grazing can reduce the abundance of important food plants in early spring (Angelstam et al. 1984, Hudson 1992) which may lower maternal condition prior to breeding (Drent and Daan 1980). This possibility was not considered within the study. Secondly, reduced grazing results in taller vegetation and hence increased cover for nests, broods and adult birds, possibly reducing levels of predation. Third, Green (1984) and Hill (1985) demonstrated a correlation between gamebird chick survival and the abundance of preferred insect foods. In these studies, low numbers of invertebrates were inversely correlated with distances moved

Table 5. Step-wise multiple regression analysis of factors explaining the number of lepidopteran larvae on bilberry. Data entered into the analysis are log transformed means of combined 1991 and 1992 values of 125 sweeps, at six replicate sites in each pinewood n=48. Significance of regression model $F_{5,42} = 41.35$, $p<0.001$

Variable	Regression coefficient	Cumulative r^2	"T" value	Sig.
Constant	4.833	0.00	11.08	$p<0.001$
Bilberry biomass log(x+1) kg m^{-2}	0.230	0.53	2.44	$p<0.05$
Log.mean annual rainfall (mm)	-1.098	0.66	-3.44	$p<0.001$
Grazed bilberry tips (%)	-0.624	0.78	-5.20	$p<0.001$
Altitude (m.ASL)	0.002	0.81	3.21	$p<0.01$
Tree density (trees ha^{-1})	0.001	0.83	2.54	$p<0.05$

Table 6. The density of Black Grouse (birds km^{-2}) on ten light and ten heavily grazed moors and from two lightly and two heavily grazed pine forests.

	Light grazing mean ± S.E.	Heavy grazing mean ± S.E.	ANOVA	Sig.
Moorland				
Females km^{-2}				
1991	3.4 ± 0.8	1.9 ± 0.4	$F_{1,14} = 5.31$,	$p<0.05$
1992	3.2 ± 0.7	1.6 ± 0.4	$F_{1,14} = 6.22$,	$p<0.05$
Males km^{-2}				
1991	2.3 ± 0.5	1.6 ± 0.2	$F_{1,15} = 4.51$,	$p<0.05$
1992	2.1 ± 0.5	1.4 ± 0.2	$F_{1,14} = 4.98$,	$p<0.05$
Pine forest				
Females km^{-2}	2.5	1.7		
Males km^{-2}	1.2	1.1		

Table 7. The breeding success of Black Grouse in late-July and August 1991 and 1992 on moors with differing grazing regimes. Only moors where five or more females were located have been included in the analysis. n = number of moors.

		Light grazing		Heavy grazing			
	Year	n	Mean±S.E.	n	Mean±S.E.	ANOVA	Sig.
Brood size	1991	8	3.7±0.4	7	2.6±0.4	$F_{1,13}= 5.04$	$p<0.05$
	1992	9	4.0±0.3	6	3.7±0.4	$F_{1,12}= 1.84$	ns
Females with broods %	1991	8	66±8	7	56±10	$F_{1,8} = 0.00$	ns
	1992	9	88±3	6	75±8	$F_{1,13}= 4.99$	$P<0.05$
Juveniles /female	1991	8	2.4±0.3	7	1.5±0.5	$F_{1,9} = 8.72$	$P<0.02$
	1992	9	3.5±0.3	6	2.8±0.3	$F_{1,13}= 7.07$	$p=0.02$

by broods which in turn were inversely correlated with chick survival.

In our study, high densities of sheep and red deer were associated with a halving of total invertebrate numbers, and a particularly marked reduction in the larvae of Lepidoptera species which were known to be preferred by Black Grouse chicks (Picozzi and Hepburn 1984, Kastdalen and Wegge 1984).

Combining these two sets of results, the correlation between lower numbers of large herbivores and better breeding success of Black Grouse may arise from a combination of higher numbers of invertebrates in taller vegetation supplying more food and better protection to broods, thus simultaneously reducing both the need for large movements between suitable foraging areas and the risk of being caught by predators.

Both Black Grouse and Capercaillie have undergone particularly marked declines in western Scotland (Hudson 1989, Baines et al. 1991, Cobley and Moss 1992). The seven-fold difference in numbers of larvae from east to west encountered in this study may explain part of this decline. The climate in western Scotland has changed from more continental to more oceanic, now characterised by prevailing westerly winds and mild wet winters. This change has had an adverse effect on numbers of Lepidoptera in the last 150 years (Thomson 1980). Given that a chick foraging in a grazed forest in the west may have up to 25-fold fewer caterpillars available to it than in a relatively ungrazed forest in the east, lower chick survival could be expected, especially in years of low insect abundance. Therefore, it was perhaps not surprising that Capercaillie were absent from three of the four western forests sampled, but that reasonable densities were still found further east. Low numbers of Capercaillie in western Scotland are associated with heavy rain in June, the hatching time (Moss 1986). The causal mechanism underlying this relationship is not known, but the results of this study imply that low caterpillar numbers in areas of high rainfall could lead to poor chick survival.

The importance of variations in invertebrate abundance to breeding woodland grouse is indicated by data on three different spatial scales. On a regional scale in native pine forests, larval abundance was positively correlated with the density of female Capercaillie. On a between-moor scale, densities and breeding success of Black Grouse were higher where reduced grazing levels were associated with more invertebrates and taller vegetation. On a habitat scale, broods selectively foraged in vegetation types which supported more invertebrates.

Table 8. Mean vegetation height and number of invertebrates caught per 25 sweeps at locations of Black Grouse broods less than two weeks old and at random sites on moorland in Perthshire (Scotland) and the Pennines (England). 95% confidence limits are given in brackets. MANOVA: Perthshire $F_{6,84} = 2.88$, $p<0.02$, Pennines $F_{6,26} = 3.20$, $p=0.02$.

	Mean nos. of invertebrates			
	Perthshire		Pennines	
	Sites with broods (n=22)	Random sites (n=82)	Sites with broods (n=13)	Random sites (n=39)
Vegetation height (cm)	41	26	30	20
Araneae	2.8 (1.9-4.0)	2.2 (1.7-2.8)	1.6 (0.6-3.1)	1.6 (1.1-2.3)
Diptera	5.6 (4.0-8.8)	3.5 (2.7-4.4)	13.4 (7.5-23.2)	9.7 (6.6-14.1)
Coleoptera	3.5 (2.6-4.5)	2.0 (1.5-2.5)	1.6 (0.9-2.5)	1.0 (0.6-1.4)
Hymenoptera	1.8 (1.2-2.7)	0.6 (0.4-0.8)	3.0 (1.7-4.9)	1.5 (0.9-2.3)
Hemiptera	7.7 (5.0-11.5)	3.8 (2.9-4.9)	19.1 (12.1-29.8)	10.2 (7.3-14.1)
Larvae *	3.5 (1.2-7.9)	1.1 0.7-1.8)	2.4 (1.4-3.5)	1.4 (0.8-2.2)
Total	38 (28-52)	21 (18-24)	49 (35-70)	34 (27-43)

* Lepidoptera and Symphyta larvae

Little can be done to change the effects of climate, but habitat improvement resulting from reductions in the numbers of grazing herbivores may go a long way to restoring numbers of woodland grouse. Low levels of grazing were associated with a more diverse habitat providing more preferred food plants, more cover for nesting and more insects to chicks.

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Summary

Reductions in the quality of habitats occupied by woodland grouse associated with differences in grazing management were assessed on 20 moors and in eight native pine forests in northern Britain. Moors with higher intensities of grazing had vegetation, on average, 32% shorter. Grazed forest had less heather and a lower biomass of bilberry than ungrazed forest. Heavily grazed habitats were associated with up to three times fewer invertebrates, particularly the lepidopteran larvae preferred by grouse chicks. Regional differences in larval abundance were correlated with the density of Capercaillie. Highest densities of both male and female Black Grouse were found on lightly grazed moors and in forests where deer numbers had been reduced. The results suggest that the presence of good ground cover with high numbers of preferred insects may allow Black Grouse to survive in situations where they would otherwise be killed by predators.

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Habitat characteristics of brood-rearing sites of Hazel Grouse *Bonasa bonasia* in the eastern Alps (Friuli-Venezia Giulia, Italy)

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Introduction

This paper presents observations on habitat use and selection by female Hazel Grouse *Bonasa bonasia* with broods, and discusses how changes in forest management and agricultural practices influence Hazel Grouse habitats in the eastern Alps.

For a long time, there have been fewer studies of Hazel Grouse in the Alps and in most European countries than of other species of grouse. Researches tended to emphasize a considerable decline in the eastern alpine population from the mid 1950s on. Hazel Grouse disappeared in the western Italian Alps about the end of the last century but, from the mid 1940s, a small population settled again in Val d'Ossola, in the eastern Piedmont (de Franceschi 1992).

Forest management is important for the conservation and preparation of suitable Hazel Grouse habitats. The species may be considered " an ideal model species" for demonstrating the importance of a certain type of sylviculture and the failure of another type in improving habitat characteristics and in increasing Hazel Grouse numbers (Swenson and Danielsen 1991). In Finland, forest management has demonstrated that it is possible both to increase the Hazel Grouse density and to produce timber and wood fibre (Swenson and Danielsen 1991). Frequent and proper cuttings of mixed woods, bringing about regeneration and the maintenance of forest habitats, were successfully proposed and experimented in the USA to support Ruffed Grouse *Bonasa umbellus*, a close relative of Hazel Grouse (Gullion 1982).

Study area

The field work was done in some mixed conifer-deciduous woods of the Central Carnia (46o 31' N, 12o 57'E), Canal del Ferro (46o 31' N, 13o 12'E) and Tarvisio Forest (46o 30' N, 13o 32' E) in the Eastern Alps. Throughout the study areas, both the brood rearing sites (BRS) and the control sites (CS) were located in a discontinuous wooded belt at 830 and 1540 m ASL in uneven-aged stands. All sites selected for study were distributed irregularly inside the mixed woods and the mean incline of slopes varied greatly from one sample area to another (from 0° to 35°).

We followed Oberdorfer (1990) in our description of the successional forest stages and the alliances found in the study area. Most BRS were located in a fragmented belt including mixed woods of spruce, fir, larch and beech, belonging to the Fagion alliance (Anemone-Fagetum association). In a few cases, sample areas were referable to the open pure spruce woods, belonging to the Vaccinio-Piceion alliance. Brood rearing sites also included at the same time two stages of the forest succession, such as Atropion alliance (most herbaceous), Sambuco-Salicion alliance (mostly shrubby) and, on moist sites, Alno-Ulmion or Tilio-Acerion alliance (an advanced stage of the succession). However, in the forest districts of the eastern Italian Alps, it was not easy to define and classify the stand typologies; 92% of the brood rearing sites belonged to the ecotonal stages of the forest and only 3 of them (8%) could be ascribed to a pure stand typology (pure spruce woods).

Material and methods

In summer 1991-92, we assessed sites where a female Hazel Grouse had successfully raised a brood in at least one of the previous 3-4 years. Sites at which broods were studied were selected from chance discovery and from repeated contacts with broods in the same sites, in summer (from early June to the end of August). Applying the minimum convex polygon method to observations, we found the centre of the polygon by connecting the external point of every contact and surveying around this point.

Twenty-five brood rearing areas were investigated, all attended by females with chicks before brood dissolution. Gamekeepers and foresters showed us some broods, but most were found during our frequent surveys in the study area. Twenty-five randomly sited control areas in nearby woods were also examined. The centre of each control site was located within forest parcels where no Hazel Grouse had been found during the previous 3 - 4 years, and more than 200 m from the centre of a brood rearing site. We assumed that the summer home range of a brood was included in the area defended by one male (c. 10-12 ha wide, according to Haga et al. (1987) and Glutz (1985)). In Sweden, home range diameter (assuming round home ranges; sexes averaged) was 470 m for Hazel Grouse (Swenson 1991, 1992). We used the distance 200 m, assuming that a female with a brood would not move out of this area, but we are not sure about this because Lieser and Eisfeld (1992) recently found in the Schwarzwald that the home ranges (described as minimum convex polygons) of one male and two females ranged from 52 to 76 ha. The surface of all grid cells (0.25 ha) actually used by these radio-located birds was about 30 ha. Moreover, in a Scandinavian forest, the summer home ranges of two broods varied from 20 - 30 ha, which means a 500-600 m diameter circle (Swenson, pers. comm.).

The habitat characteristics and vegetational variables (species, number and age of trees, overstory and understory cover, altitude, exposure and inclination of slopes) were assessed within a 0.1 ha (diameter c. 36 m on an even surface) in each BRS and in as many CS.

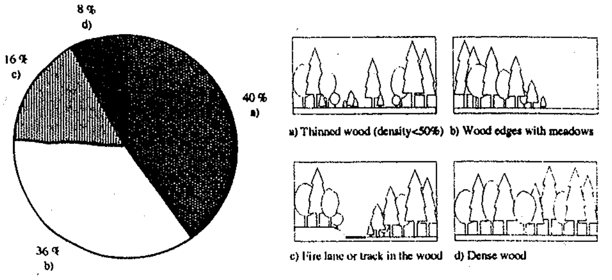

Fig. 1. Distribution of brood rearing sites in different types of forest.

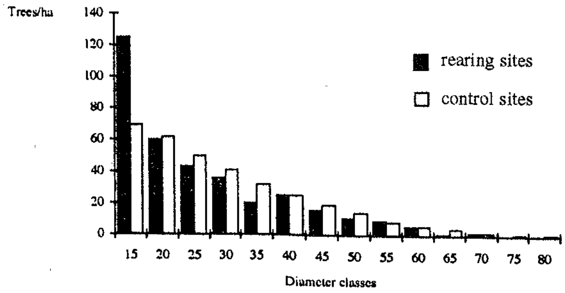

Fig. 2. Curves of diameter classes (in pentads) in brood rearing sites and in control sites.

Results

Most (76%) brood rearing sites were in managed mixed woods, and the others (24%) included some poor (i.e. at high altitude) or young woods (10 - 30 years old), naturally regenerating on formerly cultivated meadows.

Many brood rearing sites (56%) were in mixed conifer-deciduous woods frequently interspersed with natural or artificial openings (Figs. 1a, 1c). Some others (36%) were on the edge of the meadows (Fig. 1b), and only 8% were in dense woods. Small rivers or ponds were located near or within some brood rearing sites (16%). In the BRS, the tree layer (Table 1) was mainly composed of conifers (248 trees ha-1): spruce *Picea excelsa* 60%, larch *Larix decidua* 5.6%, fir *Abies alba* 3.5%, Scots pine *Pinus sylvestris* 0.1%; and broadleaved (110 stems ha^{-1}): beech *Fagus sylvatica* 23% and other deciduous 7.8% (Table 1). The mean overstory density was lower in the BRS than in the nearby randomly selected CS, both as regards the degree of canopy closure (42% vs 73%) and mean basal area (23 vs 27 m^2 ha^{-1}). The overstory density of the BRS varied from 14 - 74% and the basal area from 7 - 44 m^2 ha^{-1}.

The mean understory density (Table 2) was higher in the BRS (35%) than in the CS (21%). Natural regeneration comprised conifers (16% versus 13%) and broadleaved (19% vs 8%). Differences were observed also in the mean number of species (5.6 vs 3.9), in the frequency of species of the rich nitrogen moist soils (88% vs 21%) and grasslands (54% vs 16%) and in the extent of bare areas (36% vs 14%) (statistically significant).

In the BRS, the curves of the diametrical classes (in pentads) of the trees show a dominance of the lower classes and a high trend towards the uneven-aged structure of the stands (Figure 2.). The differences in the mean number of stems ha-1 in the BRS (358) and in the CS of the surrounding forest (334) are not statistically significant.

Some differences (statistically significant) were found by comparing the composition and other vegetational variables of the stands in the BRS and the CS. In the BRS, the mean number of species was higher, both in the tree layer and, especially, in the shrub layer (Tables 1 and 2). Spruce, beech and fir were also more frequent in the BRS than in the CS. The frequencies of *Acer, Sorbus, Alnus, Salix, Corylus* were always higher in the BRS than in the CS (Table 3). Particularly in the brood rearing areas, the frequencies of *Betula pendula, Alnus incana, Salix* spp. *Corylus avellana* and *Sorbus* spp. were much higher than expected and differences are statistically significant (Mann-Whitney U-test: U = 12; p<0.05).

Table 1. Vegetational variables of the overstorey (mean height >8m) in the study area.

	Mean cover %	Mean no. of trees/ha			Mean basal area (m^2/ha)			Mean no. of species	Meam diameter classes (no./ha)		
		conifers	broadleaved	total	conifers	broadleaved	total		<30	35-50	>55cm
Brood rearing sites	42	248	110	358	18	5	23	3.1	264	72	18
Control sites	73	234	97	331	18	9	27	2.6	222	90	22

Table 2. Vegetational variables of the understorey (mean height <8m) in the study area.

	Mean cover %			Mean no. of species	Herbaceous layer (% frequency)				% Bare ground
	conifers	broadleaved	total		shade lovers	woody perennials	herbs in most soils	grasslands	
Brood rearing sites	16	19	35	5.6	92	46	88	54	36
Control sites	13	8	21	3.9	94	40	20	16	14

Table 3. Frequency of deciduous tree species in the study area.

	Fagus sylvatica	Acer pseudoplatanus	Sorbus spp.	Alnus incana	Salix spp.	Corylus avellana	Sambucus spp.	Other deciduous
Brood rearing sites	82	20	48	36	48	36	8	20
Control sites	80	10	14	2	6	8	2	2

Table 4. T-test statistical analysis (SAS/STAT™) of some vegetational variables of the BRS and CS. (*** = very highly significant (p <0.001); ** = highly significant (p <0.01); * = significant (p < 0.05); n.s. = non-significant (BTO Guide 22)).

Variable	Mean diff.	Std. error	T-test	Significance level	
Overstory					
Mean cover	-31.72	3.8589809	-8.2197868	p = 0.0001	***
No. of species	0.48	0.2457641	1.9530923	p = 0.0626	n.s.
Understory (mean cover)					
Conifers	3.0616	3.5805777	0.8550576	p = 0.4010	n.s.
Broadleaves	10.8304	3.0928228	3.5017849	p <0.002	**
Total	13.88	4.7093241	2.973444	p <0.01	**
No. of species	1.68	0.660101	2.5450651	p <0.05	*
Bare ground	21.72	3.8177306	5.6892438	p = 0.0001	***

Table 5. Discriminant function analysis of some vegetational variables of the BRS and CS.

Variable	Standard D.F. coefficients	r (*)
Mean cover:		
Overstorey	-0.50	-0.877
Broadleaved	0.027	0.344
Understory total	0.41	0.336
Bare ground	0.56	0.587

Peculiar value	Canonical correlation	Chi square	D.f.	p
2.23	0.831	53.91	4	0.0001

Percentage of correct classification	BRS = 84%	CS = 96%

(*) Correlation coefficients between discriminant variables and D.F.

Analysis, using PROC.MEANS in SAS (1988) and one way ANOVA, revealed statistically significant differences between BRS and CS for five out of seven vegetational variables (Tables 4 and 5). Overstory mean cover and bare ground width had a high significance level (p = 0.0001). Differences were also significant between the understory variables: broadleaved density (p <0.002), total mean cover (p <0.01) and mean number of species (p <0.05). However, differences between conifer density and the number of species of the overstory were statistically non-significant.

Four vegetational variables were distinguished between BRS and CS by Discriminant Function Analysis (DFA). The most important variable in the discrimination was the overstory cover which was lower in BRS than in CS. Other important discriminating variables were bare ground, broadleaved and understory cover (Table 5).

Discussion

All the sample areas were periodically subjected to more or less intensive human activities from forestry or cultivation. Formerly, sylviculture tended to concentrate on afforestation with species of economic interest (mostly conifers). Broadleaved trees, belonging to the secondary (but sometimes also to the dominant) vegetational layer, were often neglected or felled during brashing and thinning. More recently, because of the reduced economic importance of timber, fellings tended to change to a system of felling only mature trees, creating small clearings, usually not larger than 2 ha, irregularly dispersed in the forest. Therefore, at present, in the Tarvisio Forest, and in many other districts of the Alps, sylvicultural practices do not cause great habitat changes and tend to maintain an irregular forest structure. In the Alps, in poor quality even-aged stands, more or less regularly managed with selective cuttings (or subjected to snow-breakages), the first successional stages can last up to 20 - 30 years. The rotation usually takes 80 - 120 years or more, with fellings in four stages: thinnings (10 - 20 years before the end of the rotation), seed cutting (at the end of the rotation), removal cutting (10 - 30 years after the seed cutting, to improve natural regeneration) and final cutting (30 - 40 years after seed cutting by felling only mature trees) (De Franceschi and Bottazzo 1991). All the BRS were found in regularly managed woods, or close to the edges of forest tracks, ski trails or ski facilities, and/or in meadows naturally or artificially reforested in the last 20 - 40 years.

At times, some types of "interference" can persist for a long time (as for instance, the cultivation and the mowing of meadows within the wooded montane belt (Fig. 1B), or the maintenance of roads and fire lanes (Fig. 1C)). The transitory vegetation observed in these cases lasts for years, even if maintained only in narrow strips or in small fragmented openings. Throughout the Alps, all these types of modification occurred when agri-sylvicultural practices ceased.

Differences between diameters of trees in the BRS and the CS were not significant, but the number of stems/ha belonging to the first class (12.3 to 17.5 cm) was 44% higher in the former than in the latter (127 vs 70). The structural complexity of the dominant layers, as already observed above, was always higher in the BRS than in the CS (Fig. 3).

The distribution curve of the diameter classes observed in the study area was similar to the results obtained in 23 sample areas in the Cansiglio Forest (Venetian Prealps) (Tocchetto 1993), even though these sample areas included sites where adults, broods and young were settled. All these surveys confirmed that Hazel Grouse used above all young classes of the forest and the edges of meadows, openings or clearings, both in the Cansiglio Forest and in our study areas, similar to the results obtained also in the Bohemian Forest (Klaus 1991) and in Bavaria (Scherzinger 1976).

The number of trees and shrubs and the frequency and number of secondary deciduous species such as Sorbus spp. *Alnus* spp., *Salix* spp. and *Corylus avellana* were also significantly higher in the BRS than in CS. This varied composition of stands is typical of the first forest successional stages, with a reduced overstory and understory cover, and a high frequency of young trees.

Analysis of the correlations between statistically significant variables and the canonical discriminant functions showed that the mean overstory cover and the bare ground frequency were the most important factors to identify and separate the BRS from the CS. Moreover, regarding the B-coefficient (Logistic Regression), graphics of the distribution of BRS and the CS suggested that 96% of the CS and 84% of the BRS were correctly classified (Table 5). The results of the classification showed that 21 BRS and 20 CS had a high probability (0.75 to 1) of being what they actually were. From this, it is possible to predict vegetational variables which define the habitat characteristics of Hazel Grouse brood rearing sites.

The significant differences concern the overstory mean cover ($p = 0.0001$ - Table 4) and mean cover in the understory (Broadleaves $p < 0.002$, and Total $p < 0.01$ - Table 4) and frequencies of perennial plants, herbs, grassland and bare ground frequencies (Table 2), and the deciduous species frequency ($p < 0.05$ - Table 3). All these show a higher biodiversity in the BRS than in the CS. Thus, irregular vegetational cover (allowing a greater insolation of the ground, improving a suitable herbaceous cover density and increasing the availability of insects and invertebrates) provides the best conditions of feeding (fruits, berries and arthropods) and shelter for growth of young Hazel Grouse.

Human activities can worsen or improve the habitat characteristics of the Hazel Grouse. Clearcuttings and wide monospecific conifer cultures have caused the disappearance of the species from several districts of Central Europe (Bergman et al. 1982, Klaus 1991). Consequently, fellings should be carried out with the aim of respecting, maintaining and/or restoring the composition and structure of uneven-aged mixed woods in the Alps in order to provide suitable habitats for Hazel Grouse.

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Summary

The structure and the vegetational composition of 25 summer habitats used by female Hazel Grouse and their broods in the breeding season were analysed in the Carnic Alps (from central Carnia to the Tarvisio Forest). Comparisons were made between the vegetational characteristics collected in small sample areas (100 m^2) where broods were found in summer, and in 25 randomly selected control sites. Hazel Grouse females with broods settled in uneven-aged mixed woods of spruce, fir, larch and beech belonging to the *Anemone-Fagetum* association. The overstory density was 358 trees ha^{-1} (considering ø more than 12.5 cm a.b.h.), with only 233 trees ha^{-1} (excluding those with ø less than 17.5 cm a.b.h.). The mean frequency of the

number of the tree and shrub species was higher within the brood rearing sites (BRS) than in the control sites (CS). The main differences between some forestry variables connected with the forest successional stages and forest management in the BRS and in the CS are discussed.

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Evaluation of Hazel Grouse habitat in the Black Forest (southern Germany) and implications for habitat management

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Introduction

In many parts of central Europe the Hazel Grouse *Bonasa bonasia* is in danger of extinction (Swenson and Danielsen 1991). In the state of Baden-Württemberg (Southern Germany), the Hazel Grouse population has declined from c. 400 pairs estimated in the early 1960s to c. 40 territories now, all in the Black Forest, with a big contraction in range and fragmentation (Asch and Müller 1989, Suchant 1993). There is consensus that declines of most Hazel Grouse populations are caused by habitat degradation (e.g. Asch and Müller 1989, Lieser 1990, Schatt 1991). However, few data exist to quantify this loss of suitable habitat.

In a previous study in three different areas in the Black Forest, habitat selection and the annual diet of wild Hazel Grouse were investigated by means of radio-telemetry and faecal analysis (Lieser and Eisfeld 1991, Unseld 1991, Lieser 1993). Hazel Grouse showed a pronounced seasonal shift in both habitat and diet. Food in the immediate vicinity of cover proved to be the determinant of habitat quality throughout the year. That study enabled us to define the seasonal habitat requirements of Hazel Grouse. We distinguished between winter, summer and autumn habitat. In winter and early spring, Hazel Grouse utilized stands with Norway spruce *Picea abies,* mostly pole-sized, containing a proportion of trees or bushes providing catkins as winter food. Summer habitat was characterized by a well-developed herbaceous ground layer under deciduous trees and bushes, with gaps allowing light to penetrate to the ground level. Autumn habitat, used from late summer, provided berries under or close to cover, such as young spruce. In summer and autumn, Hazel Grouse were often observed on forest roads. In dry periods, moist sites with fresh vegetation were preferred.

Pieces of adequate habitat were patchily distributed in the areas examined. Measured as utilized squares in a 50x50 m grid, the area actually used by a single bird was about 30 ha. The corresponding home range, measured as minimum convex polygon, was up to 80 ha (Lieser and Eisfeld 1991).

Based on these results, we investigated the supply of suitable habitat for Hazel Grouse in the Black Forest (Mann 1993). The purpose was to find the reasons for the decrease of the population and to recommend ways for improving the habitat. Starting from the assumption that areas inhabited by Hazel Grouse still contain adequate proportions of all habitat types required throughout the year, we compared such areas with others that were recently abandoned by the species, and with reference areas where Hazel Grouse had been absent for more than 12 years.

Study area

The study area was the present range of Hazel Grouse in the central and southern Black Forest from 47°36'to 48°18'N, and 7°40'to 8°20'E, at 400-1493 m ASL. The topography is diverse with steep slopes, hilltops, and plateaux at high altitude. The mean annual temperature varied between 4° and 8° C and the mean annual precipitation between 900 mm and more than 1800 mm, depending on elevation and exposition.

Montane forests composed of silver fir *Abies alba,* beech *Fagus sylvatica*, and sycamore *Acer pseudoplatanus*, with local admixture of Norway spruce, were the dominating natural forest community. The actual vegetation depended strongly on management, with monocultures of spruce, Douglas fir *Pseudotsuga menziesii,* silver fir and beech, mixed stands of various composition as well as different stages of plant succession on abandoned pastures and on openings caused by windthrow.

Material and methods

Sample plots

Field work was done in summer 1992 on circular sample plots of 400 m diameter (12.6 ha), based on records of Hazel Grouse compiled by the Working Group on Hazel Grouse in the Black Forest (Arbeitsgruppe Haselwild Baden-Württemberg). These records concern results from intensive search by some members of the group as well as incidental observations from other persons. Sample plots were placed in three categories of areas:

* 'occupied areas' with records of Hazel Grouse within the last three years (1990-92) (n=46)

* 'abandoned areas' with records in 1980-89 (Asch and Müller 1989), but not since 1990 (n=36)

* 'reference areas' without records since 1980 (n=39).

'Occupied' areas included all recent records except one. 'Abandoned' and 'reference' areas refer to sample plots within or adjacent to the current distribution of Hazel Grouse.

The centre of a sample plot was either:

- the centre of the home range of four radio-tagged birds
- the point of observation in the case of isolated observations
- the point of the last observation in the case of several records assumed to belong to the same home range, or
- a randomly chosen point from a grid placed over the study area in the case of the reference areas.

Sample plots in abandoned or reference areas were dismissed if their centre was closer than 1.5 km to a recent Hazel Grouse observation. The same was true for sample plots touching unforested areas.

On all sample plots (n=121, 1500 ha), type of habitat and estimated size were assessed for each tract considered suitable habitat for Hazel Grouse.

Criteria for Hazel Grouse habitat

Based on our previous results we defined the criteria for five habitat types, as follows.

1. Summer habitat - stands dominated by deciduous trees or bushes, interspersed with gaps, having a well-developed shrub layer composed of deciduous species covering at least 50% in the closed parts of the stand, and having a ground layer covering at least 30% of the total area.

2. Autumn habitat - thickets of conifers mixed with bushes providing berries (*Sambucus racemosa, Sorbus aucuparia*), making up at least 20% of the number of stems, *or* stands with a canopy closure of at least 50% and a ground layer covering at least 30%, including *Rubus* species with a cover of at least 15%, *or* areas covered with at least 10% fruiting bilberry *Vaccinium myrtillus* under or closer than 5 m to spruce cover.

3. Winter habitat - stands dominated by conifers, with a minimum of 5% of hazel *Corylus avellana*, birch *Betula pendula* or *B. pubescens* or alder *Alnus glutinosa, A. viridis* or *A. incana, or* strips of such *Betulaceae* growing closer than 5 m to spruce stands providing cover.

4. Moist sites - groves with streamlets or depressions, with a minimum width of 10 m, and shrub layer and ground layer as in summer habitat *or* with a maximum width of 10 m, ground layer as in summer habitats, and surrounded by forest edge rich in cover on at least 50% of the edge.

5. Forest roads - verges with grass, herbs or shrubs adjacent to forest edge rich in cover *or* roads covered with grass and crossing younger stands with a high amount of cover.

Data analysis

The proportion of the five habitat types was calculated for each of the 121 sample plots. The total amount of suitable habitat was the sum of all habitat types. Sections belonging to two habitat types (e.g. summer habitat and moist sites) were recorded twice, so that the total proportion of suitable habitat exceeded 100% in one case.

The results are presented graphically. Figures 1-6 show the proportion of suitable habitat of each of the sample plots for each habitat type. Within the three categories, the sample plots are sorted by decreasing values. The abscissa is scaled in percentages and shows the proportion of sample plots reaching a given level of suitable habitat. Differences between the samples were tested according to Kolmogorov-Smirnov (2-tailed, $p \leq 0,05$), using the greatest difference of the proportion of sample plots (horizontal distance between two curves in the figures) to calculate the test value.

Results

Only a part of the sample plots in all three categories contained suitable habitat in quantities worth mentioning. Within this group (left hand sides of Figures 1-6), obvious differences exist between the categories. When no suitable habitat of a given type was found, the lines converge to zero in the right halves of the graphs. For comparisons, two characteristic values of each curve are given below.

The median proportion of summer habitat (Fig. 1) was 4.1% (occupied areas), 4.3% (abandoned areas), and 1.4% (reference areas). Less than 1% summer habitat was found in 26% of the areas currently inhabited by Hazel Grouse, in 31% of the abandoned areas, and in 44% of the reference areas. The only significant difference was between the occupied and the reference areas.

No significant differences were found between the amounts of autumn habitat (Fig. 2). The median values were 0.8% (occupied areas), 1.2% (abandoned areas), and 1.0% (reference areas). Fifty-four percent, 47% and 51% of the sample plots had practically no autumn habitat (less than 1%).

Winter habitat (Fig. 3) had median values of 1.0% in both the occupied and reference areas and 0% in abandoned areas. Fifty percent of the areas inhabited by Hazel Grouse, 61% of the abandoned areas, and 51% of the reference areas had less than 1% winter habitat. No differences were statistically significant. Nevertheless, differences between the curves are obvious. The eight sample plots with more than 20% winter habitat are all in 'occupied' areas.

The proportion of suitable habitat on moist sites or along forest roads (Fig. 4 and 5) hardly exceeded 5% of a sample plot. The median values for 'moist sites' were 0.4% (occupied areas), 0.4% (abandoned areas), and 0% (reference areas), for 'forest roads' 1.0%, 0.9% and 0.3%. Fewer than 1% suitable moist sites were found in 65% of the occupied areas, in 64% of the abandoned areas, and in 85% of the reference areas. Forty-eight percent, 53% and 90% of the sample plots had less than 1% of suitable habitat along forest roads. In the case of the 'forest roads', the distribution of the reference values was different from the occupied areas as well as from the abandoned areas.

Figure 6 shows the sums of suitable habitats on the sample plots. The median proportion was 25.7% in the occupied areas, 11.0% in the abandoned areas, and 6.8% in the reference areas. Hardly any Hazel Grouse habitat (less than 5%) was found in 19% of both the occupied and abandoned areas, and in 39% of the reference areas. The difference between the occupied areas and the reference areas was statistically significant.

Fig. 1-6. Proportion of sample plots (x) containing a given proportion of suitable Hazel Grouse habitat (y) for sample plots in occupied areas (∗), abandoned areas (+) and reference areas (▪). Each signature represents a single sample plot.

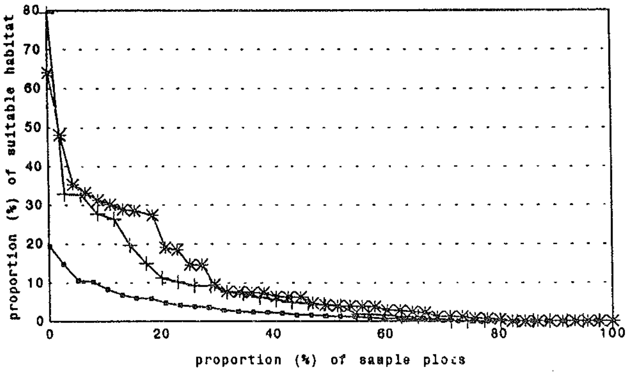

Fig. 1. Summer habitat.

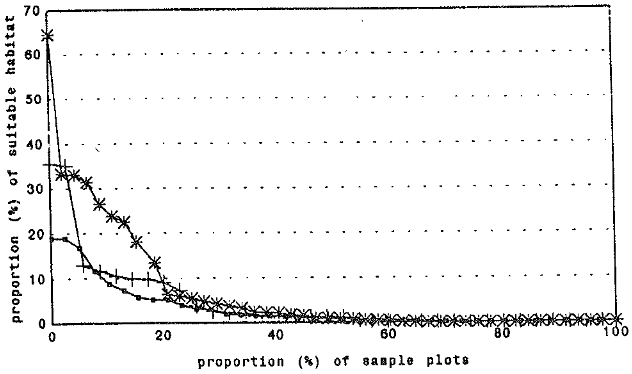

Fig. 2. Autumn habitat.

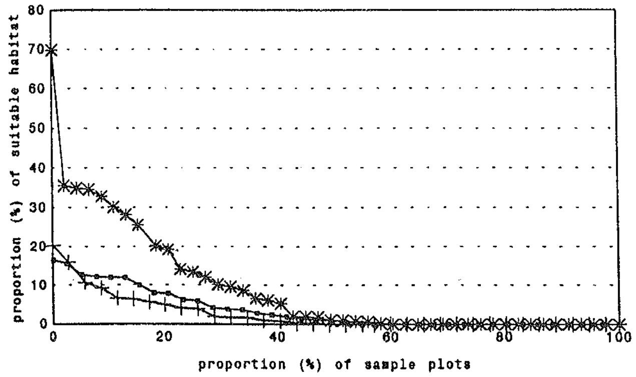

Fig. 3. Winter habitat.

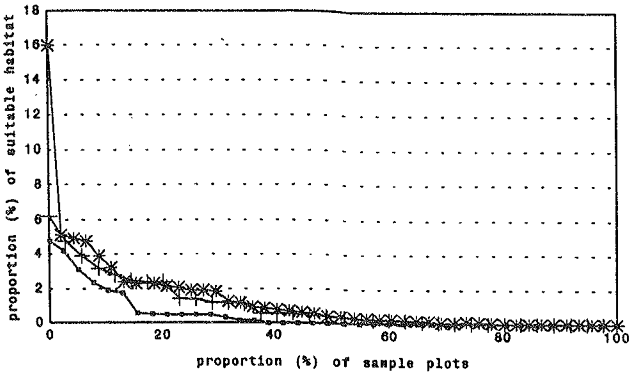

Fig. 4. Suitable moist sites.

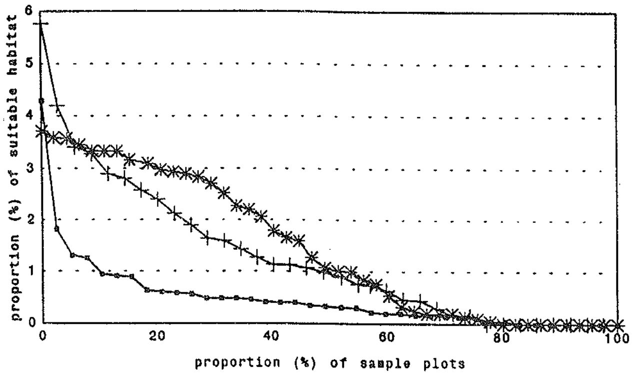

Fig. 5. Suitable habitat along forest roads.

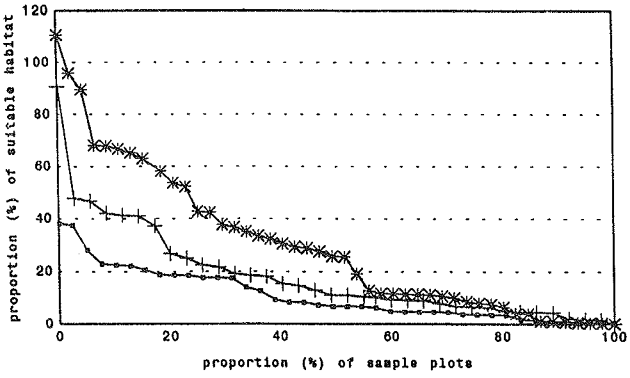

Fig. 6. Sum of suitable habitats.

Discussion

Habitat as determinant of Hazel Grouse occurence

Areas with and without Hazel Grouse (occupied and reference areas) showed differences in the composition of the forest. Each habitat category considered to be favourable for Hazel Grouse was less abundant in the reference areas, but these differences were statistically significant only for summer habitat, suitable roadsides, and the sum of all habitat types considered. This suggests that at least one cause of the decrease of the Hazel Grouse population in the Black Forest was habitat degradation. The proportions of suitable habitat in areas recently abandoned by Hazel Grouse ranged more or less between those of the occupied and the reference areas. In the abandoned areas, the process of habitat deterioration seems to be less advanced than in the reference areas, but habitat quality is no longer sufficient for Hazel Grouse.

Three major processes have led to the decrease of habitat quality for Hazel Grouse in the Black Forest.

- Intensive management of younger stands in favour of tree species of main economic interest (spruce, silver fir, Douglas fir, beech)
- Maturation of former Hazel Grouse habitats (coppice woods, former pastures left to succession)
- Conversion of such non-productive woodland into monocultures of conifers.

These factors are considered to be responsible for the decline of the Hazel Grouse in many parts of central Europe (Faber 1987, Lieser 1990, Klaus 1991, Schatt 1991).

Because Hazel Grouse use (we conclude for the Black Forest that use means need) rather different habitat types during different seasons, an area will lose its suitability as Hazel Grouse habitat as soon as one of the essential habitat types falls below the minimum level required. The identification of this limiting habitat type should facilitate appropriate management measures. Unfortunately, our data give no hint to such a specific bottleneck. All habitat types examined show a decrease of similar extent from ‘occupied’ through ‘recently abandoned’ to the ‘reference’ areas.

The search for the limiting habitat type leads to the question of the minimum proportion of the total area which essential habitat types must attain to fulfill the requirements of Hazel Grouse. If sample plots in occupied areas were representative for Hazel Grouse home ranges, the proportion of each of the essential habitat types in these areas should be at least adequate. Our results, however, do not allow such an interpretation; a considerable proportion of the sample plots in occupied home ranges contained no or little Hazel Grouse habitat in the different categories.

Several methodological shortcomings may explain this result. First, the sample plot may lie outside or only partly inside a Hazel Grouse home range. This could occur, a) if the observation that was the basis for situating a sample plot concerned a Hazel Grouse outside its home range (e.g. a juvenile bird during dispersal), or b) if a bird was at the edge of its home range, or c) if another species of bird was mistaken for a Hazel Grouse (e.g. Woodcock *Scolopax rusticola*), or d) if the location was mapped incorrectly by the observer. Secondly, the sample plots (12.6 ha) covered just a part of the total home range (up to 80 ha). With the patchy distribution of suitable habitat components found in the Black Forest, it is likely that certain habitat types present in a particular Hazel Grouse home range were not adequately represented in the corresponding sample plot.

Furthermore, the criteria for ‘suitable’ habitat may be inadequate and thus the inventory of habitats incomplete. At high altitude, buds of rowan *Sorbus aucuparia* for example may perhaps replace catkins of *Betulaceae* as winter food, or coniferous stands rich in bilberry might serve as summer habitat. On the other hand, abandoned or reference areas may show proportions of suitable habitat that are sufficient for Hazel Grouse. Suitable habitat may be over-represented in a sample plot, with the surrounding forest being inhospitable for Hazel Grouse. The potential home range belonging to such a sample plot will then contain too little suitable habitat. Or a suitable area may be too isolated from occupied areas so that the probability of being colonized by dispersing birds is too small. This may explain why many sample plots in abandoned and reference areas show higher proportions of suitable habitat than plots in occupied areas.

For these reasons, our data cannot be used for deriving minimum area requirements of Hazel Grouse for the different habitat types. Nevertheless, such lower limits will exist. And it is conceivable, with the differing proportions of suitable habitat in the three categories of sample plots, that Hazel Grouse in the occupied areas may still find enough suitable habitat throughout the year, whereas in the abandoned areas, and more so in the reference areas, at least one seasonal habitat type may no longer be available in the quantity required.

Implications for habitat management

To manage forests to encourage Hazel Grouse, we need to preserve and increase suitable habitat for all seasons of the year to increase the probability that Hazel Grouse will find appropriate conditions for survival and reproduction. Detailed recommendations for such management are given by Unseld (1991), Suchant (1993, 1995) and Lieser (1993). Here, only the rough outlines are discussed.

The availability of winter habitat depends on how the young stands are tended. If the elimination of species providing catkins (hazel, birch, alder, willow *Salix sp.*, aspen *Populus tremula*, which occur in high numbers in areas of regrowth) is stopped and pruning of conifers is confined to future crop trees, enough stands with winter food and cover in close proximity will again be available, even in intensively managed forests.

To improve summer habitat is more difficult. In former times, coppice woods offered the required structure in large areas. Conservation and regeneration of the remnants of this type of forest is expensive and usually confined to small areas of private land. Another source of good summer habitat is certain stages of natural succession, for instance on abandoned range land or in areas with windthrow. Again, this kind of management, or better non-management, mostly means some loss of income from forestry.

In intensively managed forests, summer habitat can develop in thickets and pole stands of deciduous trees that let more light pass to the forest floor than does beech, the most common deciduous crop. The extension of the cultivation of such species, especially ash *Fraxinus excelsior* and sycamore, will therefore benefit Hazel Grouse. Few data exist concerning the suitability of such stands for chick rearing (Zakrzewski 1993). Their classification as summer habitat was based on their use by adult Hazel Grouse during these months. Possibly, our criteria for summer habitat were not sufficiently stringent to identify areas that allow successful reproduction. Suitable habitat for chick rearing may be the key factor for the survival of the population.

Suitable moist sites are a special kind of summer habitat that plays a role especially during dry periods when in other places the ground layer becomes sparse. Because moist areas are less suited for timber production, they lend themselves to special management for Hazel Grouse, e.g. by leaving them to natural succession.

Species providing catkins and trees and shrubs producing berries occur in ample numbers in tracts of regrowth. To create autumn habitat, we must avoid the elimination of these food plants when forests are brashed, or their loss by shading in dense stands without gaps, or their oppression by browsing wild ungulates. The impact of browsing on grouse habitat is also discussed by Eiberle and Koch (1975), Lieser (1990) and Klaus (1991).

Forest roads with their low vegetation, which receives a fair amount of insolation and which is situated directly adjacent to tree cover, are in principle favourable for Hazel Grouse. If we provide for a diversified vegetation and suitable cover along the verges, they can serve as additional summer and autumn habitat. Due to their linear nature, roads, as well as the strips along forest streams, are good means for linking patches of suitable habitat which otherwise are isolated by tracts of forest hostile to Hazel Grouse.

Our recommendations for managing the forest in favour of Hazel Grouse are, in many respects, in accord with the new general concept of ecologically adapted silviculture of the Forest Administration of Baden-Württemberg. Therefore, there is a good chance for their realization, and thus a hope that the population of Hazel Grouse will survive in the Black Forest.

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Summary

We investigated habitat selection and the annual diet of wild Hazel Grouse in three study areas in the Black Forest, we also determined seasonal habitat requirements. Based on these results, the forest structure on 121 sample plots of 12.6 ha each was analysed and habitat quality was evaluated. The sample plots represented areas inhabited by Hazel Grouse, areas recently abandoned by Hazel Grouse, and randomly chosen reference areas.

Median proportions of suitable summer habitat, autumn habitat, and winter habitat were 4.1%, 0.8% and 1.0%, respectively, for occupied areas; 4.3%, 1.2% and 0% for abandoned areas; and 1.4%, 1.0% and 1.0% for reference areas. Road verges and moist sites with a multi-layered vegetation provided additional food and cover for Hazel Grouse and thus complemented the other habitat types. Median proportions of the total of suitable habitats were 25.7%, 11.0% and 6.8%, respectively.

Our data show differences in habitat quality between the three categories of sample plots giving a plausible explanation for the occurrence or absence of the birds. The data did not allow us to determine a limiting habitat type or the minimum amount of habitat required for a Hazel Grouse home range. However, it is evident that habitat quality in forests abandoned by Hazel Grouse has decreased due to silvicultural activities. Implications for managing Hazel Grouse habitat are discussed. The recommended management measures fit into the general programme of ecologically adapted silviculture in Baden-Württemberg.

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Evaluation of habitat suitability for Capercaillie *Tetrao urogallus* in the northern Black Forest

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Introduction

Numbers of Capercaillie *Tetrao urogallus* in the northern part of the Black Forest have decreased over several decades to the early 1980s. For future management, an assessment of habitat conditions in the commercial forests and prediction of changes in the near future were required.

In the core Capercaillie areas in the Black Forest, the birds avoided forests with closed canopy (Ganter 1974). Open forests were usually rich in bilberry *Vaccinium myrtillus*, and bilberry seemed to be a key for evaluation of Capercaillie habitat. Wittlinger and Roth (unpublished) formed a first evaluation method, and this was improved for the northern Black Forest in the Wildbad Capercaillie project (Schroth 1990).

The aim of this study was to test this evaluation method in an adjoining area with a stable Capercaillie population, and to determine the most important habitat parameters for evaluation.

Study area

The study was done from July to October 1990 in the state-owned forest of Kaltenbronn in the northern Black Forest. This was a compact woodland of about 34 km^2. Capercaillie occured on the upper slopes and on the plateaux (850-1000 m ASL) with forests dominated by Norway spruce *Picea abies* with some silver fir *Abies alba* and Scots pine *Pinus sylvestris*. The field layer was dominated by bilberry, some grasses and mosses. On the plateaux, there were large bogs covered with mountain pine *Pinus montana*.

The climate was humid with annual precipitation 1500 mm and mean annual temperature 6.5°C. The red sandstone formed poor and acid soils with bogs on the plateaux.

In the study area, the Capercaillie density was c. 2-3 birds per km^2.

Methods

For evaluation of the forest stands, the field layer was classified in five classes (Table 1) from optimal food and cover with high diversity (class 1) to class 5 which was unsuitable for Capercaillie (Schroth 1990). Food was estimated as bilberry cover, and shelter as the proportion of the field layer which was at least 20 cm deep. Table 1 shows stands of different tree types. The medium term trend of habitat suitability was estimated and drawn on the map with the respective signs, given in Table 1.

In habitats used by Capercaillie in the northern Black Forest, there were few decidous trees and Scots pine was always available in the higher mountains, so tree composition was not considered for evaluation.

Habitat selection by Capercaillie was studied using circular random areas in the maturing and mature stands for searches for droppings, feathers and other signs, dividing the study area into two successional stages (Table 2). Younger stands (avoided by Capercaillie) and bogs (no commercial forest) were less important for this study, and therefore excluded in the results. It was assumed that these signs gave good indices of habitat use. The radius of the sample circles and the distance between two circles were varied to get approximately the same number of circles in each stratum, representing about 5% of the stratum area respectively.

For each sample, the following habitat parameters were described - cover of bilberry, height of bilberry, cover of tree layer, age and habitat suitability. In addition, each sample circle was searched for Capercaillie droppings, tracks, roosting trees, sandbaths and feathers (Porkert 1975).

Droppings including many needle fragments, lasting from November to spring (Wilhelm 1982, Storch et al. 1991), showed habitats used in winter, and observation of birds showed habitats used in summer. Doubtful findings were rejected. Droppings from the previous winter could still be identified in late summer and autumn.

Apparent differences in habitat use were tested by chi-squared statistics and correlations by Spearman's rs. Two-by-two tests were corrected for continuity using the Yates correction (Weber 1986). Bonferroni Z statistics were used to compare habitat use with availability of single classes (Neu et al. 1974, Marcum and Loftsgaarden 1980).

The ratio between the number of samples with findings and the total number of samples was called the probability of findings and was used to demonstrate preferences in the single classes.

$$\textit{Probability of findings (\%)} = \frac{\textit{No. of samples with findings} \times 100}{\textit{No. of all samples}}$$

Evaluation of former habitats

The first detailed descriptions of each forest stand in Kaltenbronn were made in 1843 and were repeated every ten years. From these data, habitat quality in former times can be evaluated. Forest descriptions from 1843, 1854, 1873, 1913, 1933, 1954 and 1973 were used. The actual habitat suitability was estimated in the field by comparison with the different classes of food, cover and stand structure (Table 1).

Table 1. Evaluation method for Capercaillie habitat (Schroth 1990).

	Food: cover of bilberry	Shelter: cover of field layer (≥ 20 cm)	Structure of stand: edges, openings, multi-layered	Sign (see below)
Class 1 - optimal	> 50 %	very good	very rich	+++
Class 2 - good	20-50 %	good	rich	+++
Class 3 - still suitable	< 20 %, grasses and herbs	less good	less rich	++
Class 4 - less suitable	sparse bilberry	poor	poor	- - -
Class 5 - unsuitable	no field layer	poor	uniform	- - -

Signs (indicating the medium term trend):

+++ (green)	Stand with increasing habitat quality, that probably will be evaluated with a higher class in 10 years.
++ (black)	Suitability of stand can be increased short-term by forestry habitat management.
- - - (black)	Stand with decreasing habitat quality, that probably will be evaluated with a lower class in 10 years.

Explanation for the evaluation method:

bilberry	bilberry with young shoots and berries.
shelter	cover of ground vegetation, which was at least 20 cm deep.
structure	estimated by eye; rich structured habitats of class 3 to 5 were evaluated one class higher, poor structured habitats of class 1 and 2 were evaluated one class lower.
class 3	the field layer was usually dominated by grasses and herbs and young forest trees, forming shelter.

Table 2. Sample design.

Successional stage (age in years)	Area (ha)	Number of samples	Radius of sample circles (m)	Distance between circles (m)
maturing stand (50-100 years)	789	131	30	240
mature stand (> 100 years)	1.221	144	35	280

Results

Field layer

Bilberry was the main important plant in the field layer. Capercaillie avoided stands with less than 20% cover of bilberry during the whole year (Fig. 1, $p<0.05$, $p<0.001$). In the summer, stands with 20-40% bilberry cover were preferred ($p<0.001$), but not in the winter. The most preferred stands had more than 40% bilberry cover. In the preferred summer habitat, bilberry shrubs were at least 20 cm deep ($p<0.01$).

Preferred summer habitats had shelter in the field layer covering at least 50% of the area (Fig. 2, $p<0.001$). Stands with less than 25% shelter were avoided ($p<0.001$). In the winter, there was no significant difference in use.

Forest structure

Capercaillie avoided uniform forests ($p<0.001$) whereas they used two-layered stands in summer ($p<0.05$) and multi-layered stands in winter ($p<0.05$). Maturing and mature stands ≥ 850 m ASL with uniform structure were more closed ($p<0.01$) and therefore poor in bilberry

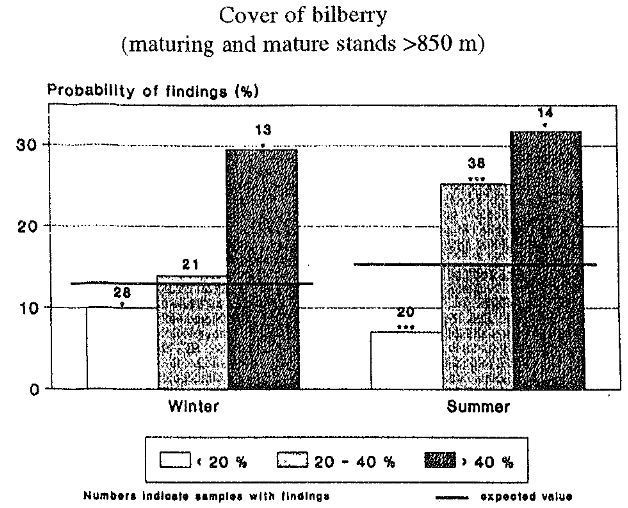
Cover of bilberry
(maturing and mature stands >850 m)

Fig. 1. Habitat selection of Capercaillie in summer and winter in relation to the cover of bilberry.

(p<0.05). Multi-layered stands were more frequent in older forests (rs=0.9 p<0.05).

Forests with natural regeneration were preferred in summer (p<0.01) and were richer in bilberry (p<0.01), whereas clearcuts of more than 1 ha size were avoided (p<0.001).

In summer, edges of old stands, including small stripe clearcuts, with natural regeneration and bilberry, were much used. Here there were more bilberry shrubs than on clearcuts or in stands with open canopy (p<0.001). But these habitats were only used at random in winter.

Correlations between habitat structures and habitat evaluation

Habitat analysis in the study area showed significant differences in habitat use in several parameters between males and females and between summer and winter use (Schroth 1993). However, the evaluation method makes no difference between sexes or seasons.Therefore we had to test if the habitats of Capercaillie were well evaluated by this method.

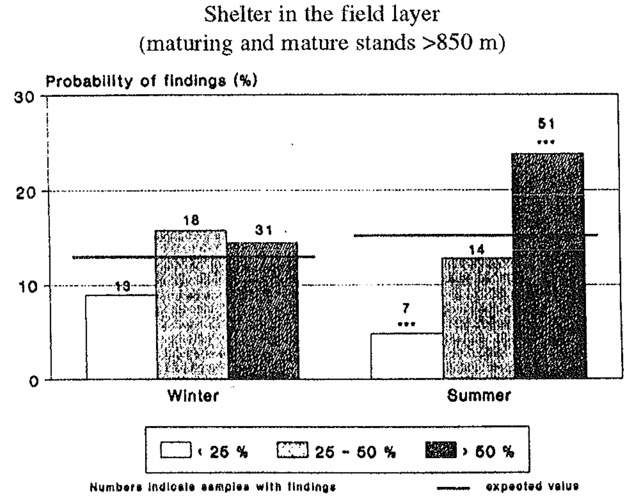
Shelter in the field layer
(maturing and mature stands >850 m)

Fig. 2. Habitat selection of Capercaillie in summer and winter in relation to shelter in the field layer.

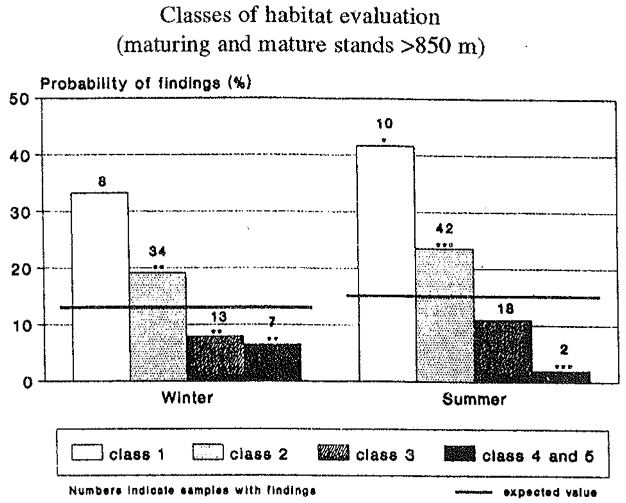
Classes of habitat evaluation
(maturing and mature stands >850 m)

Fig. 3. Distribution of the habitats selected by Capercaillie on the classes of the habitat evaluation model.

In each sample circle, the forest was evaluated according to this method (Fig. 3). There were no significant differences in habitat use of the 5 classes between males and females or between summer and winter. For the whole year, forests in class 1 and 2 were preferred (rs=1.0, p<0.01).

All correlations shown in Table 3 underline the key role of the cover of bilberry for the evaluation of Capercaillie habitat.

Habitat change in Kaltenbronn since beginning of forestry

Based on detailed descriptions of all stands, repeated every 10 years since 1843, changes in Capercaillie habitat for the Kaltenbronn forest were studied and the whole forest area, including bogs, was evaluated. Figure 4 shows the decline of optimal and good habitats and the expansion of less suitable and unsuitable forests with increasing impact of forestry. The main decrease of these habitats was in the 20th Century with heavy cutting of old stands after the war. In the last decade, habitat quality has improved.

Discussion

The study confirmed the suitability of the evaluation method. Habitat parameters such as age of forest or topography (Eiberle 1976, Klaus et al. 1985) were correlated with the cover of bilberry in Kaltenbronn (Schroth 1993) as well as parameters of habitat structure (multilayered, rich in borderlines, openings).

Improvement of the evaluation model

The field study suggests some corrections for the evaluation model. A detailed evaluation should use all five classes. But classes 4 and 5 were avoided in summer and class 4 was randomly used in winter. It is possible to evaluate the habitats used in the whole years with these five classes.

Table 3. Correlation between habitat parameters of maturing and mature stands ≥ 850 m and the cover of bilberry.

Parameters	Cover of bilberry Spearmans rs	
Cover of field layer	0.94	p<0.01
Shelter in the field layer	0.94	p<0.01
Canopy closure	-1.0	p<0.01

Table 4. Evaluation model for Capercaillie habitat.

	Food: Cover of bilberry	Shelter: Cover of field layer (≥ 20 cm)
Class 1	> 40 %	> 50 %
Class 2	20-40 %	> 25 %
Class 3	< 20 %, grasses and herbs	> 25 %
Class 4	< 10 %	0-100 %
Class 5	< 5 %	0-100 %

Explanations for the evaluation model:

bilberry	bilberry with young shoots and berries.
structure of stand (edges, openings multi-layered)	estimated by eye; rich structured habitats of class 3 to 5 are evaluated one class higher, poor structured habitats of class 1 and 2 are evaluated one class lower.

The study shows that the limit between level 1 and 2 can be changed to 40% cover of bilberry instead of 50%. The 20% minimum cover of bilberry for good habitats was confirmed by this study. Shelter on the ground can be evaluated as in Table 4. At least one quarter but better half the field layer should be covered by shrubs, grasses and herbs that are 20 cm deep or deeper.

Table 4 shows the improved evaluation model. Habitats are evaluated using a combination of "food" (estimated as cover of bilberry) and "shelter" (estimated as plant cover on the ground ≥ 20 cm deep). The study of the Kaltenbronn habitat shows that Capercaillie prefer forests with at least 20% bilberry cover and a dwarf shrubs layer that is 20 cm or more deep. Although both these parameters were positively correlated in the study area, it seems to be more reliable to estimate shelter separately, as additional shelter from herbs, grasses and natural regeneration in other areas can also be evaluated with this method.

The structure of a stand was estimated by eye. Rich structured habitats of level 3 to 5 were evaluated one level higher, whereas poor structured habitats of level 1 and 2 were evaluated one level lower.

For a quick evaluation, a 3-level model can be used, where the preferred habitats (level 1 and 2) form the high level and the less or unsuitable levels 4 and 5 the low level. Level 3 was habitat selected at random and was constant.

This evaluation model was developed in the northern Black Forest and is valid for Capercaillie habitats there. For use under other geological and climatic conditions the model probably has to be adjusted.

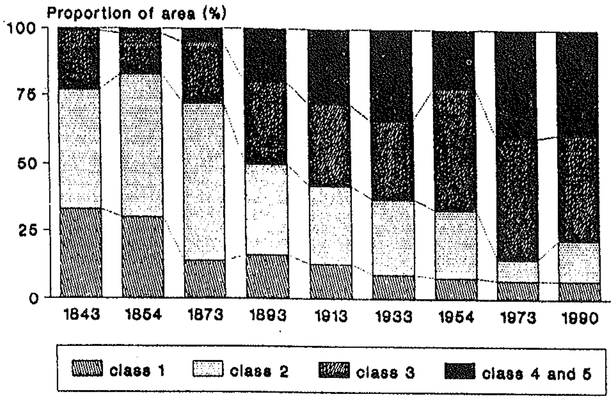
Changes of Capercaillie habitat in Kaltenbronn

Fig. 4. Capercaillie habitat change in Kaltenbronn since beginning of forestry in 1843, evaluated with the method of Schroth (1990). (class 1 = optimal habitat; class 2 = good; class 3 = still suitable; class 4 = less suitable; class 5 = not suitable)

Use of habitat evaluation for habitat management systems

Habitat evaluation in the study area showed that core areas should have at least 15-20% of forests at level 1 and 2, and at least 50-60% with level 1-3 (Schroth 1990). Such woods have good sub-populations of Capercaillie if they are > 200 ha and connected with other sub-populations. There we find several leks (Angelstam 1986, Rolstad and Wegge 1987). The core habitats should be not more than 5 km distant (Müller 1988) and should be connected to them with step stones that are at least 50 ha in size. Step stones are typically situated in higher elevation on ridges (Roth and Nievergelt 1975, Schroth 1990).

Critical situations for sub-populations result from isolation and decrease in suitable habitat in the core areas. Therefore it is necessary to evaluate the actual situation and the middle term trend of the habitat. Management plans can then be created as a part of the forest plan.

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Summary

From experience with Capercaillie in the northern Black Forest, which showed the importance of bilberry *Vaccinium*

myrtillus and of old, open multi-layered woods containing trees of different ages, a model for Capercaillie habitat evaluation was formed and tested in the field, using food and cover as estimators of suitability. Habitat maps were drawn to demonstrate the effects of fragmentation. These maps can be used as a basis for habitat management in forestry. Habitat changes during the last 150 years were evaluated with this model, using the detailed forest descriptions of former decades.

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The role of bilberry in central European Capercaillie habitats

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Introduction

Capercaillie *Tetrao urogallus* are generally viewed as being associated with bilberry *Vaccinium myrtillus*. Bilberry occurs in most Capercaillie habitats, is abundant in the species' main distribution range, the boreal forest, and the eastern borders of distribution of both species coincide well (e.g. Klaus et al. 1989). Bilberry is the main food source of Capercaillie during summer and autumn (for review see Jacob 1987). Recently, the birds' preference for forests rich in bilberry has been documented by radio telemetry in the boreal forest (e.g. Rolstad 1988), and in central Europe (Storch 1993 b, c). In contrast to the boreal forest, bilberry cover varies strongly at both the local and the landscape scale in central European Capercaillie habitats. This offers a good opportunity to analyse the role of bilberry in habitat relationships of the Capercaillie.

In this paper, I aim to show that the distribution of bilberry at the landscape scale may influence habitat and range use by Capercaillie not only during the snow-free seasons, but throughout the year. Furthermore, I analyse the abundance of bilberry in relation to forest structure, and discuss implications for Capercaillie conservation and habitat management in central Europe.

Study area

The study area was Teisenberg (50 km^2), a mountain range in the foothills of the Bavarian Alps, Germany (47°48'N, 12°47'E). Elevations ranged from 700-1300 m ASL in the central part, and reached 1800 m in the south. The climate was moist and temperate, with snow-cover from December to April. The forests were dominated by Norway spruce *Picea abies*, mixed with fir *Abies alba* and beech *Fagus sylvatica*. Forestry had created a mosaic of even-aged forest stands of varying size (1-100 ha) and successional stages. Due to soil characteristics, rich bilberry cover was mostly restricted to the central part of the area (Fig. 1). For a detailed description of Teisenberg, see Storch (1993 b, c).

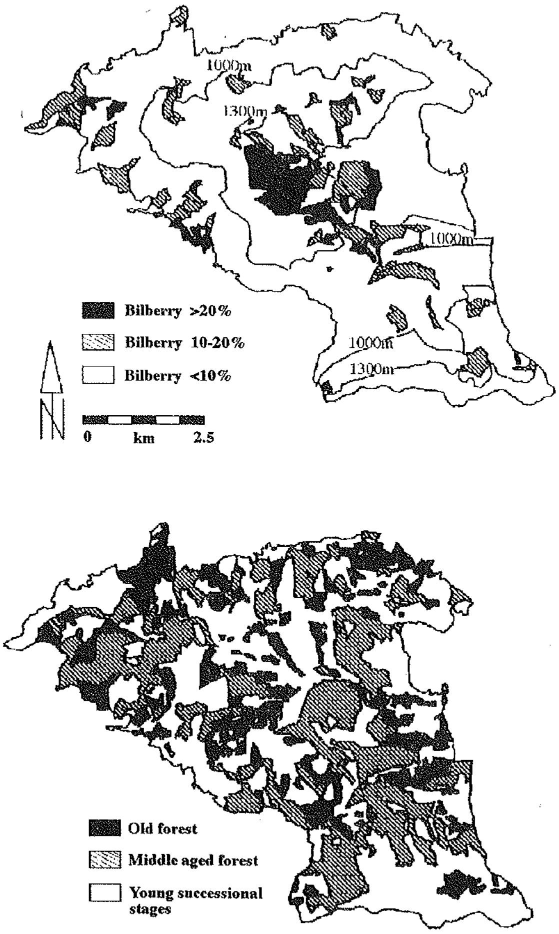

Fig. 1. Top: Distribution of rich bilberry cover (total ground cover >50% and proportion of bilberry in the field layer <10%, 10-20%, and >20%, respectively) on Teisenberg. Bottom: Distribution of old and middle aged forest.

Material and methods

The analyses are based on individual annual home ranges of seven females and 19 males radio-tracked for one full year between 1988 and 1992. The birds were located by triangulation from distances <1 km; locations with error polygons >1 ha were excluded from analyses of habitat selection. Annual home ranges were estimated as 100% convex polygons, based on 112-356 ($\bar{x}$=203) fixes, excluding locations with error polygons >5 ha. The seasons were subdivided as winter (December - March), spring (April - May), summer (June - August), and autumn (September - November).

Forest stands were classified as clearcut (covered by natural regeneration), thicket (young forest before thinning), pole stage (after first thinning, c. 20-50 yrs old), middle-aged forest (after second thinning, c. 50-90 yrs), and old forest (final felling stage, >90 yrs). Habitat availability in the study area and in individual home ranges was estimated with the help of 2500 random points distributed over a habitat map of the study area. The measures used were forest age class, mean canopy cover (%), mean height of the ground vegetation (cm), total ground cover (%), and composition of the ground vegetation (grass: *Poaceae, Juncaceae, Cyperales;* bilberry; fern: *Pteridophyta*; moss: *Bryophyta*; raspberry, *Rubus spp.;* others), expressed as the mean proportion (%) of total ground cover. For further details on methods of habitat mapping, see Storch (1993 b).

Selection of annual home ranges and habitat use within home ranges were evaluated from movements of individuals. To analyse home range selection, the mean proportion of bilberry cover in the ground vegetation of home ranges was related to availability in both the entire study area and in old forest (Wilcoxon signed-rank matched-pair test).

Seasonal habitat use was compared to availability within individual home ranges. The annual home range was assumed to be the area generally available to an individual. Therefore, availability (A) was calculated as the mean proportion of bilberry within the area of each bird's annual home range, and utilization (U) as the mean proportion of bilberry in the bird's radio locations from each season. For each bird, Ivlev's electivity index (Krebs 1989) was calculated as I=(U-A)/(U+A), and the observed electivity scores were tested against random utilization (I=0; Wilcoxon signed-rank matched-pair test).

Results

Selection of home ranges

Individual annual home ranges of females and males had similar proportions of bilberry in the ground vegetation (females: 14.5±4.2%, $\bar{x}$±SD, n=7; males: 17.4±7.1%, n=19; ns). Home ranges had greater mean proportions of bilberry than expected from availability in both the entire study area (z=-4.4, p<0.001; sexes pooled), and in old forest stands (z=-3.6, p<0.001) (Fig. 2).

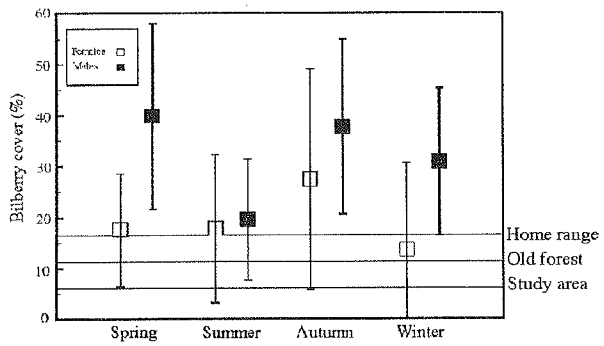

Fig. 2. Proportion of bilberry cover in the ground vegetation ($\bar{x}$±SD) at locations used by female (n=7) and male (n=19) Capercaillie, by sex and season. The background lines indicate mean bilberry cover in the entire study area, in old forest stands, and in the annual home ranges of the individuals studied.

Habitat use within home ranges

In summer and autumn, female and male Capercaillie used locations with similar amounts of bilberry in the ground vegetation. During summer, they used their home ranges randomly in relation to bilberry cover. In autumn, they selected locations with greater bilberry cover than expected from availability within the home ranges (z=-2.1, p<0.05). The proportion of bilberry cover in the ground vegetation of bird locations significantly differed between the sexes in winter (U=52, p<0.05) and spring (U=23, p<0.05), when males used locations with greater proportions of bilberry

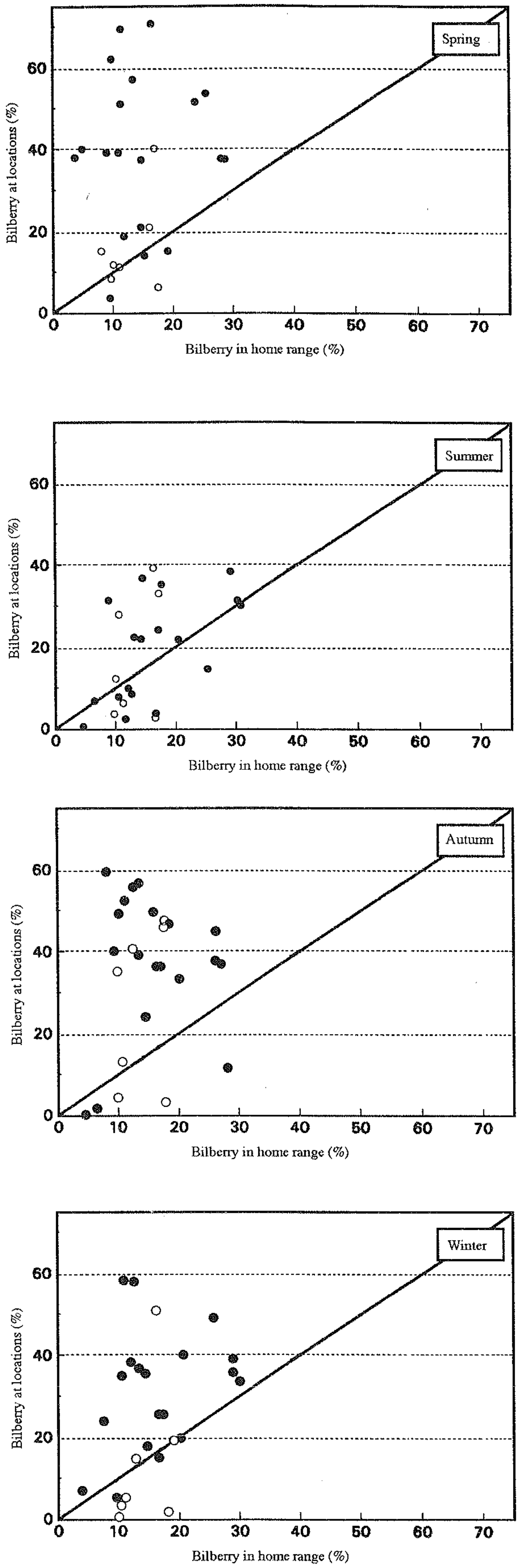

Fig. 3. Mean proportion of bilberry cover at locations of individual Capercaillie females (open circles) and males (filled circles) compared to the mean proportion of bilberry cover within annual home ranges, by sex and season. The diagonal lines indicate random use of habitats within home ranges.

than did females. Within their home ranges (Fig. 3), males used locations with more bilberry than expected in spring ($z=-3.2$, $p<0.01$) and winter ($z=-3.3$, $p<0.001$). For females, habitat use within home ranges was not significantly different from random use in spring and winter. This might have been due to small sample size, however.

In summer, males used locations with lower proportions of bilberry than in any other season (ANOVA, Duncan test; $F=6.4$, df = 3, 118, $p<0.001$). Seasonal differences in the proportion of bilberry in female locations were not significant. Compared to availability in old forest stands, males used locations with significantly greater bilberry cover than expected in all seasons (summer: $p<0.05$; other seasons: $p<0.001$) (Fig. 2).

Annual home ranges of females and males were not significantly different in size. Home range size was negatively correlated with the mean proportion of bilberry within the range ($r = -0.59$, $p<0.001$) (Fig. 4). Bilberry cover within home ranges was not correlated with any other habitat factor.

Bilberry and forest structure

Height, cover, and composition of the ground vegetation of Teisenberg varied with canopy cover, and thus with forest stage (Table 1, Fig. 5). Total ground cover ($r=-0.61$, $p<0.001$) and vegetation height ($r=-0.53$, $p<0.001$) were negatively correlated with canopy cover, and were greatest in open patches such as clearcuts. Bilberry cover was best in stands of moderate canopy cover around 50%. This corresponds best to old forest, where bilberry cover was significantly greater than in middle-aged and pole stage stands (ANOVA, $F=44.1$, df=2, 1498, $p<0.001$). However, at the landscape scale, the distribution of rich bilberry cover did not coincide with the forest mosaic (see Fig. 1). About half of the old forest area had less than 10%, and only 8% had more than 50% of bilberry in the field layer.

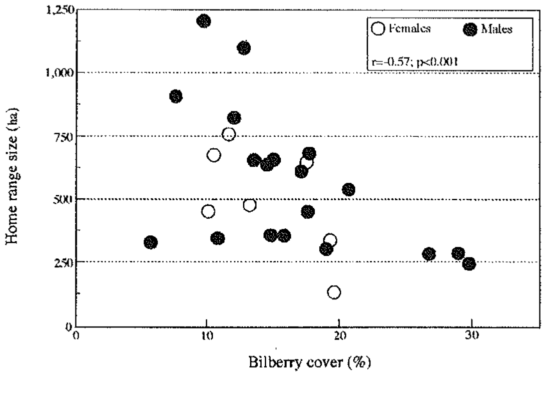

Fig. 4. Size of annual home ranges in relation to the mean proportion of bilberry in the field layer of the home range.

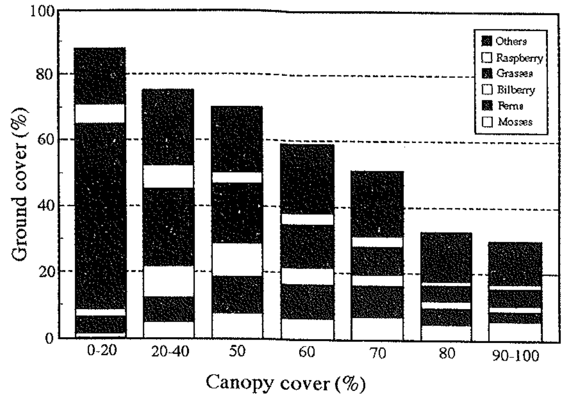

Fig. 5. Relationship between total ground cover (total height of the columns), composition of the ground vegetation, and canopy cover in Teisenberg forests (see Table 1 for explanation of vegetation types).

Discussion

The main distribution range of the Capercaillie is the Palaearctic boreal zone. At the southern edge of the range, in central Europe, Capercaillie are associated with habitats with structural features typical of the boreal forest, such as open forest structure and a well developed field layer (e.g. Klaus et al. 1989, Storch 1993a). In contrast to the boreal forest, rich bilberry cover is rare and patchily distributed, such as described for Teisenberg.

The present study shows that Capercaillie on Teisenberg were associated with forests rich in bilberry cover throughout the year. Habitat use within home ranges, however, varied seasonally. At forest stand level, Capercaillie on Teisenberg strongly preferred bilberry over all other vegetation types in summer and autumn (Storch 1993b). However, both sexes used their home ranges randomly in relation to bilberry cover in summer, although bilberry accounted for a major portion of the diet (Storch et al. 1991) (Fig. 6). In autumn, the same individuals selected bilberry-rich sites. Bilberry reached a peak in the diet in September, but quickly dropped as the season proceeded. The differences in spacing behaviour in summer and autumn may reflect a trade-off between predator avoidance and food availability. During the moult in summer, when food availability probably is generally high, the birds may spread out. In autumn, when food availability deteriorates, they

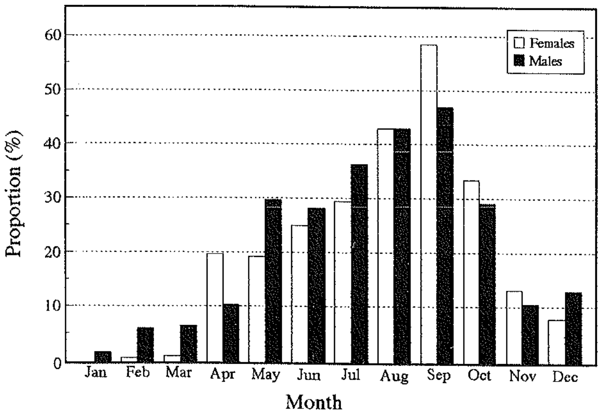

Fig. 6. Proportion of bilberry (buds, leaves, stems, berries) in the diet of Capercaillie from Teisenberg, by sex and month (data from Storch et al. 1991), as revealed from faecal analysis.

Table 1. Aspects of habitat structure by successional forest stage on the upper slopes (1000-1300 m altitude) of Teisenberg: proportion of the area, canopy cover ($\bar{x}$ ± SD), and height ($\bar{x}$ ± SD), total ground cover ($\bar{x}$ ± SD), and composition of the field layer ($\bar{x}$) (grass: *Poaceae, Juncaceae, Cyperales*; fern: *Pteridophyta*; moss: *Bryophyta*; raspberry: *Rubus* spp.).

Forest stage*	Area (%)	Canopy cover (%)	Height of field layer (cm)	Total ground cover (%)	% of total ground cover					
					Grass	Bilberry	Fern	Moss	Raspberry	Others
clearcut	9		45±25	93±16	57	3	10	2	10	19
thicket	9		22±19	46±28	31	5	12	14	7	32
pole	15	75±11	8±6	25±18	14	4	18	24	2	34
middle	31	70±10	14±8	50±18	13	5	16	14	4	47
old	21	56±11	28±13	79±14	26	11	19	8	7	30

* stands of mixed age excluded

aggregate in the area of best bilberry cover.

Spacing in winter and spring was influenced by the position of leks. This particularly held for males, which occupied winter home ranges and spring territories near to the lek centres (Storch 1993c). On Teisenberg, all four leks were located in the central part of the area, where bilberry cover was best. Presumably therefore, the strong selection for bilberry-rich sites by males in winter and spring results from the position of leks.

As in most other areas, Capercaillie preferably used old forest on Teisenberg (Storch 1993b, c). This is the forest stage with best bilberry cover. The association with bilberry-rich sites, however, is not simply a result of the birds' preference for old forest, because bilberry cover at Capercaillie locations exceeded the availability of bilberry shrubs in old forest. In contrast to other types of ground vegetation, the advantage of bilberry shrubs may lie in simultaneously providing optimal food and cover throughout the snow-free season (Storch 1993b). Therefore, forests rich in bilberry may allow the Capercaillie to minimize movements and reduce home range size, as indicated by the negative correlation between bilberry cover and home range size. Large home ranges may result in poor survival (Gjerde and Wegge 1989). The role of bilberry in population dynamics, however, remains to be studied.

At a local scale, Capercaillie may use forests without bilberry, as known from some areas of the Alps. Based on the results from Teisenberg, however, I hypothesize that the distribution of bilberry is a major cause of the distribution and density of Capercaillie at the landscape scale in central Europe (see also Storch 1993b).

Implications for Capercaillie conservation

Bilberry cover may be significantly influenced by human land use practices. In the past, Capercaillie numbers in central Europe were highest at times of intensive utilization of forests, when regular output of nutrients kept the soils poor and favoured the growth of bilberry (see review in Klaus et al. 1989, Schroth 1995). Today, there are many threats to bilberry. They span from a local to a continental scale, and include biotic as well as abiotic factors, such as forestry, browsing, and pollution (see Klaus et al. 1989 for review). Particularly due to nitrogen deposition from air and rain, bilberry is increasingly replaced by grasses (Porkert 1982, Klaus et al. 1985, Ellenberg 1983, 1992). This will reduce the quality of Capercaillie habitats, and may contribute to further population decline.

The preservation of bilberry therefore should become a key topic in Capercaillie conservation. Large-scale threats to bilberry cover, such as internationally caused pollution, will be hard to tackle. At the local scale, the growth conditions for bilberry may be significantly influenced by forestry. As my study indicates, bilberry develops best in forests with moderate canopy closure. Longer rotation periods and earlier thinning of young stands may therefore improve the abundance of bilberry shrubs. Here, cooperation between foresters and conservation biologists is needed. Adaptive habitat management experiments are desirable in order to test these ideas and to develop and improve techniques in grouse conservation.

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Summary

Although the Capercaillie *Tetrao urogallus* is well known to be associated with bilberry *Vaccinium myrtillus*, the role of bilberry in Capercaillie habitat relationships has hardly been studied. In this paper, data from a five-year telemetry study in the Bavarian Alps, Germany, were used to analyse habitat selection by Capercaillie in relation to the distribution of bilberry at the landscape scale. Capercaillie were found in areas of rich bilberry cover throughout the year. They established annual home ranges in areas with good bilberry cover, and home range size was negatively correlated with bilberry cover. Habitat use within home ranges varied seasonally; selection of bilberry-rich sites was most pronounced in autumn. Also, leks were in the areas with best bilberry cover. The results indicate that bilberry is a major factor in the distribution and density of Capercaillie at the

landscape scale. Therefore, the preservation of bilberry should become a key topic in Capercaillie conservation in central Europe.

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Silvicultural measures for the improvement of grouse habitats in the Black Forest

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Introduction

Numbers of Capercaillie *Tetrao urogallus* and Hazel Grouse *Bonasa bonasia* have been declining in the Black Forest for decades (Roth and Suchant 1990, Asch and Müller 1989) The decline has slowed for Capercaillie in the last few years, but not for Hazel Grouse (Figs. 1, 2). A "Capercaillie working group" begun in 1972 by the forest service of the state Baden-Württemberg aimed to reverse the decline of Capercaillie. In a final report in 1974, destruction of habitat was considered to be the main cause for the decline and a number of recommendations were made (Arbeitsgruppe Auerwild 1974). A second working party found predators to be important for the decline in addition to loss of habitat, climate change and disease. After five years of research, a third working group drew the conclusion that loss of suitable habitat was the most important reason for the decline in Capercaillie (Schroth and Weiss 1990). In 1989, a "Hazel Grouse working team" was founded and after four years of research it too suggested that the decisive factor for the decline of Hazel Grouse was the change of habitat (Suchant 1993, Lieser and Eisfeld 1991). This conclusion was also reached by other authors (Görner et al. 1988, Storch and Willebrand 1991, Schatt 1991, Glänzer 1992, Swenson 1991).

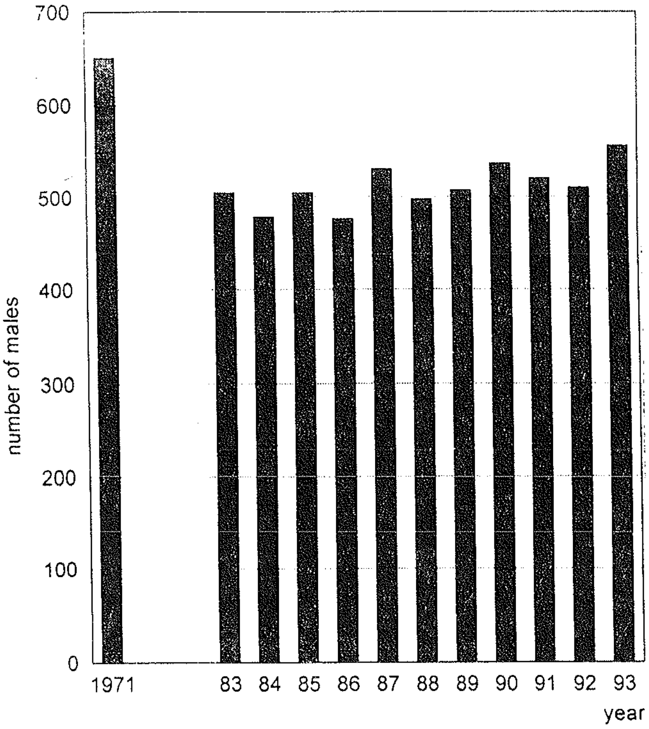

Fig. 1. Numbers of Capercaillie in the Black Forest. Source: data from annual inquiries of foresters, hunters, and ornithologists. The number of males is the total number seen in the lekking period (original data for 1990-93 from Roth and Suchant 1990).

For the last 20 years, the forest service of the state of Baden-Württemberg has considered habitat requirement of grouse species in its guidelines for forest management. Especially recently, it is suggested that forest management should follow the principles of natural forest succession. Grouse species are considered to be a characteristic of an ecologically balanced forest. If ecological concerns are integrated into silvicultural management, the new suggestions should have positive effects for grouse species too. The problem is how to implement these ideas in practical forestry. Even today, one can see a number of examples where forestry management has negative consequences on the quality of habitat for grouse species. The reason for this contradiction between defined objectives and practice in forest management is that for many decades conservation of species or habitat was considered either not at all or too little. Silvicultural methods which combine economy and ecology simultaneously can best change old considerations.

This study shows how economics can be brought into line with management for wildlife. The first example is the management of coppice forests. Coppiced woodland can be rich in wild fauna and flora. One area in the Black Forest showed an average of 51 breeding bird territories of 36 bird

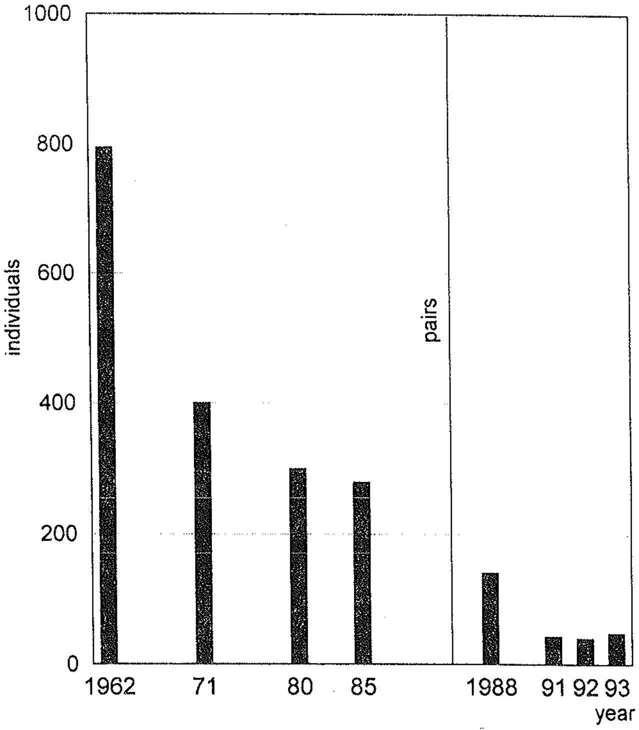

Fig. 2.Numbers of Hazel Grouse in the Black Forest. Source: Leonhard (1964) for 1962 and Roth (1987) for 1971 - 1985 give the total number of individual birds. Asch and Müller (1989) for 1988, Asch (original data for 1991) and Suchant (original data) for 1992 give the number of pairs.

Table 1. Comparison of management alternatives for coppice. Rotation, suitability as Hazel Grouse habitat and economic assessment are given for each alternative. The economic assessment gives the relationship between input and output of money.

Management alternatives	Rotation n (in years)	Suitability as Hazel Grouse habitat (% of forest area)	Economic assessment - = negative 0 = neutral + = positive
Coppice	30	80	-
Discontinued coppice system	-	50	0
Change into conifer	120	0	+
Change into mixed stands	120	30	+
Conversion to coppice forest with cherry tree standards	60	70	+

species per 10 hectares. The diversity of moths was also remarkable. One hundred and ninety-four species were caught in light traps. Two thirds were characteristic of deciduous forests, with 50 % dependent on broadleaved trees as food for the caterpillars (Freundt and Pauschert 1992). However, good floristic diversity is only found in coppiced woodlands when these are managed as such (Heinemann 1990).

In the Black Forest, coppice forms one of the last retreats for Hazel Grouse. The suitability of a forest as habitat for Hazel Grouse depends among other things on structure, texture, mixture of tree species, canopy closure and ground vegetation. These factors are determined by natural development or by forest management. In addition, forests have a dynamic development and are constantly changing. Within this dynamic development, fauna and flora keep changing. The Hazel Grouse has its ecological niche in a very short succession phase of forests which is formed by young and pioneer tree species. This young phase is maintained artificially in coppice forests by a rotation of 20 or 30 years. Every coppice forest is different and not every coppice forest provides suitable habitat for Hazel Grouse. If a coppice system is no longer managed, its suitability as Hazel Grouse habitat diminishes.

Coppicing was already known by the Romans as "silva caeduae" and reached a peak in woodland management in the second half of the 19th Century. In those times there were 20,000 ha of coppice in the Black Forest (Abetz 1955). But since the turn of the Century, coppice was converted to high forest. Today, only 6000 ha of coppice remain in the Black Forest. Distinct alternatives to the coppice system exist from the economic point of view.

A second example considers the management of young stages of high forest. A comparative study examines whether today's forest management, which is declared to be close to nature, can also fulfill the demands of habitat-improvement for Capercaillie and Hazel Grouse.

Alternative silviculture strategies for coppice forests

The following management alternatives are compared concerning both economic assessment and suitability as Hazel Grouse habitat (Fig.3 and Table 1). The suitability as Hazel Grouse habitat depends on the rotation and on the management after coppice cut. A long rotation and the loss of deciduous trees both shorten the proportion of suitable habitat for Hazel Grouse.

Management alternatives

1. Coppice system

Almost all stages of coppice development are potentially suitable for Hazel Grouse. Cover and food supply are optimal during most periods. Only a new area of clearfell is not utilizable. But not less than five years after cutting, the area will again be covered with a dense forest, 3 - 5 m in height. Coppice shoots grow very fast. If the chronological development of the different coppice phases is portrayed spatially, 80% of the coppice area is suitable as Hazel Grouse

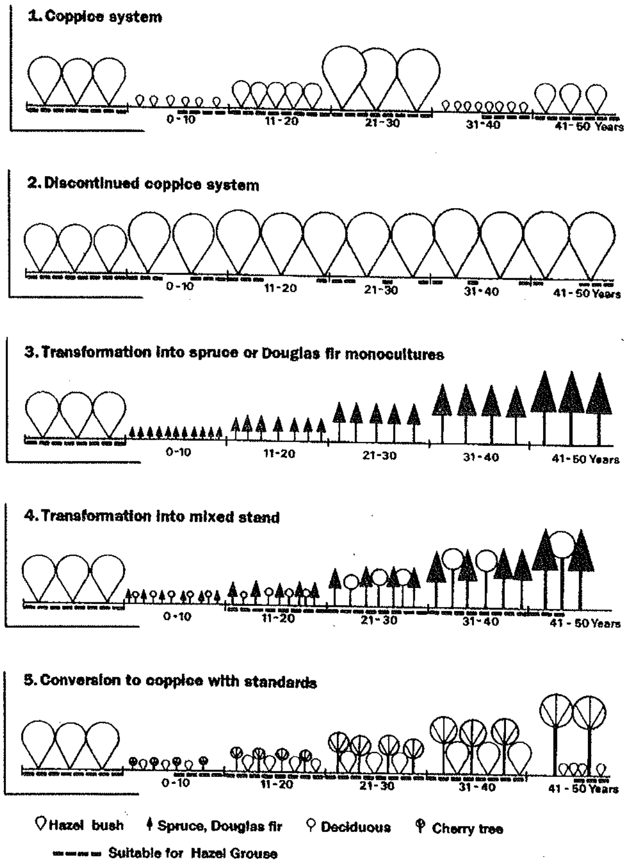

Fig. 3. Alternatives for the coppice system in relation to the suitability as habitat for Hazel Grouse.

habitat. Because only small areas of coppice are cut each year, the different phases are very close side by side. However, the economic revenue is negative, because the necessary input for the management is more expensive than the income.

2. Discontinued coppice system

If the coppice system is not continued and the sites are set aside for natural development, there will consequently be no clearcuts. But as the coppice gets older, the stumps rot, the canopy opens and cover protection for grouse is no longer perfect with an increased risk of predation.

3. Transformation into spruce or Douglas fir monocultures

This silvicultural method is the one most frequently used, but it is also a radical method. Coppice is cut, coniferous trees are planted and non-commercial species are removed. Hazel Grouse habitat is destroyed at one blow. The revenue is positive, because the income for timber is higher than the input for management.

4. Transformation into a mixed stand of coniferous and deciduous trees

The main feature is that 10 - 30% of deciduous trees or shrubs are left in the conifer stands. This proportion is sufficient to maintain the suitability of the habitat for Hazel Grouse for at least 30-40 years. Spatially, 30% of the forest area is suitable as Hazel Grouse habitat, assuming a rotation of 120 years. The economic assessment is similar to alternative 3.

5. Conversion to coppice forest with cherry tree *Prunus avium* standards

This alternative is similar to a coppice system, with the main difference that cherry trees are widely planted in the cut area. Following the management model described below, 70% of a forest managed in this way is suitable for Hazel Grouse.

Management model "coppice with cherry tree standards"

A management model has been developed for the coppice with cherry tree standards. This model takes into account ecological as well as economic concerns. It was developed and examined in two areas of coppice forests in the Black Forest at 600 and 800 m ASL.

The high economic value of cherry trees results from the combination of a high price for cherry timber, the fast growth rate and low costs. Cherry timber has a market value of 300 DM/m^3 which is a higher price than for other profitable timbers such as oak *(Querqus* spp.) or ash *(Fraxinus excelsior)* (Mahler 1988). Cherry species are pioneer trees characterised by a very high initial growth rate. On good sites, exploitable sizes can be reached within 60 years.

The following management model for coppice forests takes this economic value into consideration as well as the requirements of wildlife. On small (< 1 ha) clearcuts of coppice forests, cherry tree standards are planted in a 5 x 5 m arrangement. During the first 5 years, coppice shoots are removed if necessary within a circle of 1 m around the cherry plants. Pruning to 3 m height is carried out when the trees reach 6 m, with pruning continuing to 6 m when the trees reach 12 m. Except for this management, nothing is done till age 30, when the tree diameter has reached approximately 20 cm. At this stage, a pre-commercial thinning takes out 30-50% of the cherry stems. In the course of the thinning, coppice shoots are cut in the same way as in an ordinary coppice system. A reduction down to 100 stems/ha is done by a commercial thinning at the age of 40 - 50 years. Within a rotation of 60 years, growth up to 26 m and a volume per tree of 2.35m^3 can be accomplished (Pryor 1988).

This model is now being tested in two test sites. The study started in 1989 with the planting of 400 cherry trees on an area which was cleared of coppice. The first results show that the cleared area is utilizable by Hazel Grouse two years after the cutting, beause the coppice shoots grow very fast and give a very dense cover with a good vertical structure. Hazel Grouse were first seen in 1992.

Comparisons of alternatives to this coppice system show how decisive the type of forest management is for habitat suitability. One extreme is the destruction of habitat by monocultures of conifers. Another extreme is the optimization of habitat conditions by coppice forest management. Both extreme alternatives are one-sided and lead to either an economic or ecological impasse. Coppice with cherry tree standards has proved to be the best alternative when economic and ecological demands are combined.

Forest management in favour of grouse in comparison with today's silvicultural guidelines

The declared aim of today's forest management in Baden-Württemberg is a form of silviculture close to natural vegetation and natural cycles. This is put in place by guidelines which differ regionally, by silvicultural systems, stand types and age classes. One guideline defines possible and neccessary management for young stands, referring to stem numbers, structure and mixture of species. We did a study where we compared this official guideline with recommendations given by the Hazel Grouse and Capercaillie working groups.

The site had a size of 3.08 ha at 900 m ASL with a western exposure and a slope of 35%. The trees were 10-25 years old (average 20 years) with a height of 3-9 m (average 6 m) . Twenty-six sample circles were established, each with a radius of 2 m giving an area of 12.6 m^2 (i.e. 1.1% of the study site). The occurrence of tree and shrub species was measured according to different height classes (Scharl 1992). This represented the situation "before tending", concerning only the height class of the dominant trees (>2m) (Fig. 4). A second step determined the trees and shrubs which had theoretically to be removed according to the forest service guidelines. The theoretically remaining stand was sampled ("guidelines young stands").

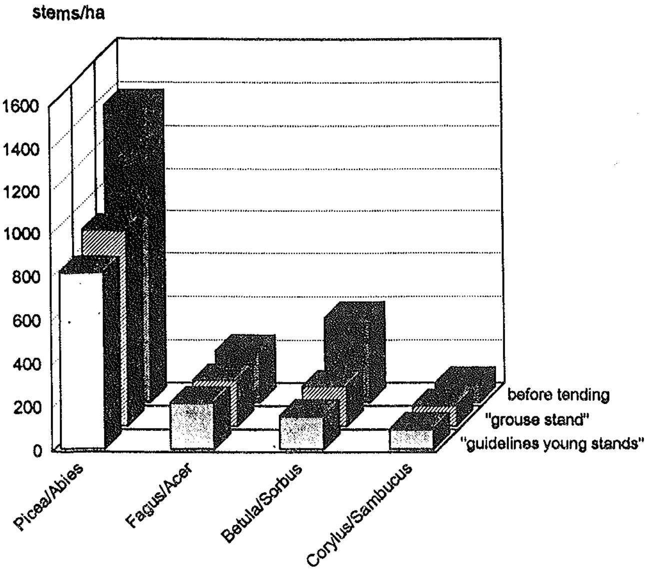

Fig. 4. Tending of young stands: comparison between tending according to general guidelines ("guidelines young stands") and tending according to recommendations of a grouse working group ("grouse stand").

In a third step, forest workers were given instructions for management which included the recommendations of the Hazel Grouse and Capercaillie working groups. The most important rules for tending were the following.

- reduction of number of spruce *Picea abies*
- preservation and promotion of associated species, especially pioneer species
- preservation and promotion of shrubs
- enlargement of bare soil patches for the stimulation of ground vegetation
- installation of 4m wide management trails with a tree cover towards the forest road

Management followed these instructions. Afterwards, the sampling was repeated. The stand was then named the "grouse stand". From all this, a comparison of today's forest service guidelines with the recommendations of "grouse people" became possible.

Results

Reduction of spruce stem number

After tending according to the recommendations favouring grouse, fewer spruce stems had been removed than the forest service guidelines demanded (Fig. 4). However, the difference was small and unimportant. In both cases, spruce remained dominant.

Preservation of associated species, especially pioneer species

Associated species came out differently. Economically important species such as beech *Fagus sylvatica* and maple *Acer pseudoplatanus* were preferred in both silvicultural treatments and as a result the stem numbers were equal. In the case of pioneer species, including rowan *Sorbus aucuparia* and birch *Betula pendula,* there were differences. According to the forest service guidelines, these trees should be removed whenever the objective of management was endangered. The objective of management was defined as the mixture of species at the end of the rotation. Every tending and thinning must lead to this objective. In our study, the mixture for the stand at the end of the rotation was defined as spruce (50%), fir (30%) and beech (20%). However, birch or rowan should be removed only if these species endangered the objective of management. Ten to twenty per cent of secondary tree species like birch or rowan in a young stand cannot endanger the silvicultural objective. In fact, 20% of secondary tree species would provide winter habitat for Hazel Grouse.

Concerning associated species, the difference between guidelines and grouse recommendations is unimportant.

Preservation of shrubs

According to the forest guidelines, shrubs such as hazel *Corylus avellana* or elder *Sambucus nigra* should be tolerated because they normally do not hinder development of the commercial tree species. Management orientated towards grouse would not only leave such shrubs but give preference to them because otherwise the shrubs would be overgrown by trees in a short period. Therefore, forest guidelines and grouse recommendations are different. In our case, this difference is negligible.

Summarizing, tending of young stands according to today's forest service guidelines also fulfils the demands of habitat management for grouse.

Discussion and conclusions

The decline of grouse species has continued for decades in the Black Forest due to loss of suitable habitat. To improve grouse habitat, it is first necessary to connect silviculture management with the demands of grouse. Today, silvicultural methods are required which are adapted to all requirements of society and which take site characteristics into account. Silviculture must be a result of a balance which has to include different viewpoints such as timber utilization, recreation and nature conservation. It is in this context that the relationship beween silviculture management and grouse habitat must be considered.

The main question is whether recommendations for the improvement of grouse hahitat can be integrated with modern forestry practices. Forest owners demand economic profit. This study shows ways in which economic matters can be brought into line with wildlife management. One example is the management of coppice forests. The comparison of management alternatives results in a management model "coppice with cherry tree standards", which has proved to be the best alternative when economic and ecological demands are combined.

Modern forest service guidelines aim to create suitable habitats for grouse because grouse species are considered to be characteristic of an ecologically balanced forest. These guidelines are a part of a silviculture which is declared to be close to nature. A first thinning experiment in a mixed stand compares these official guidelines with the recommendations of the grouse working groups. The result of this experiment is an improvement of grouse habitat, when the outlines are implemented in practical forestry.

Summary

Numbers of Capercaillie and Hazel Grouse have been declining in the Black Forest for decades. For Capercaillie, but not for Hazel Grouse, this trend has slowed during the last few years. The loss of suitable habitats is considered to be the cause of this decline, associated with other unfavourable factors such as predators, changes in climate and tourism. Silviculture management influences the suitability of forests as habitats. To improve grouse habitats, it is first necessary to convince the forest rangers through combining cash flow and wildlife management simultaneously. This paper discusses the basic silvicultural objectives with regard to grouse habitat and gives two practical examples for the combination of financial gain and good wildlife management. One example is re-afforestation with cherry trees in new coppice forests. One of the last retreats of Hazel Grouse in the Black Forest is in ancient coppiced woodland. For economic reasons, these woods are now being transformed into monocultures of spruce or Douglas fir. Cherry timber production is an economic alternative with the advantage of maintaining Hazel Grouse habitat.

The other example is a management experiment in a mixed stand, mainly involving a reduction in spruce and an increase of pioneer species. The official guidelines of today's silviculture are compared with the recommendations for habitat management by a grouse working group.

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Other papers

Distribution of grouse in the Italian Alps (1988-1992)

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The distributions of breeding grouse in the Italian Alps were mapped over five years(1988-92) as "Certain", "Probable" or "Possible" using 1:25,000 topographic maps produced by the Istituto Geografico Militare (IGM). Each map covers an area about 10 km x 10 km, and the entire Italian Alps include 643 of these maps.

Aims and methods

This study aimed to locate nesting areas and determine altitudinal limits of the species of grouse that occur in the Italian Alps. I used the international standard method of estimating the breeding range of species, as established by the European Atlases Ornithological Committee (EOAC) (Sharrock 1973). Percentages given for distribution (Table 1) are the proportions of all the maps in which the species was recorded. Besides grouse, the study also described distributions of Rock Partridges *Alectoris graeca* and mountain hares *Lepus timidus*. The atlases covering the entire Alpine chain result from a synthesis of all provincial atlases, plus that of Stelvio National Park (Artuso 1994). Data on altitude, obtained throughout the year were grouped into sectors, formed by provinces, as follows.

Western sector : Savona to Vercelli
Central sector : Novara to Verona (excluding Bolzano)
Eastern sector : Vicenza to Trieste
Alpine Chain : includes all the Italian Alps where altitudinal surveys were made (data obtained from all the three sectors).

Table 1. Proportions of maps in which grouse species were reported.

Hazel Grouse	46% (292 maps occupied)
Ptarmigan	54% (345 maps occupied)
Black Grouse	82% (526 maps occupied)
Capercaillie	40% (255 maps occupied)

Table 2. Altitudes at which grouse and Rock Partridges were recorded.

Species	Sectors and Alpine chain	Nos. of observations	Altitude (m)			Preferred altitudinal belt (m)
			Mean	Min	Max	
Hazel Grouse	Western	-	-	-	-	-
	Central	33	1663	900	2000	1500 - 2000
	Eastern	239	1250	550	2000	1100 - 1700
	Alpine Chain	272	1300	550	2000	1050 - 1650
Ptarmigan	Western	48	2415	1750	3000	2200 - 2600
	Central	55	1973	1500	2450	1800 - 2100
	Eastern	55	1885	1000	2450	1800 - 2300
	Alpine Chain	158	2077	1000	3000	1800 - 2400
Black Grouse	Western	216	1719	420	2400	1500 - 1900
	Central	245	1576	500	2100	1500 - 1900
	Eastern	665	1510	650	2400	1300 - 1900
	Alpine Chain	1126	1564	420	2400	1450 - 1850
Capercaillie	Western	-	-	-	-	-
	Central	20	1590	800	2000	1500 - 2000
	Eastern	318	1323	500	2000	1200 - 1700
	Alpine Chain	338	1338	500	2000	1200 - 1700
Rock Partridge	Western	205	2016	1100	2930	1700 - 2300
	Central	124	1588	400	2500	1400 - 2000
	Eastern	181	1152	415	2300	700 - 1500
	Alpine Chain	510	1605	400	2930	1000 - 2100

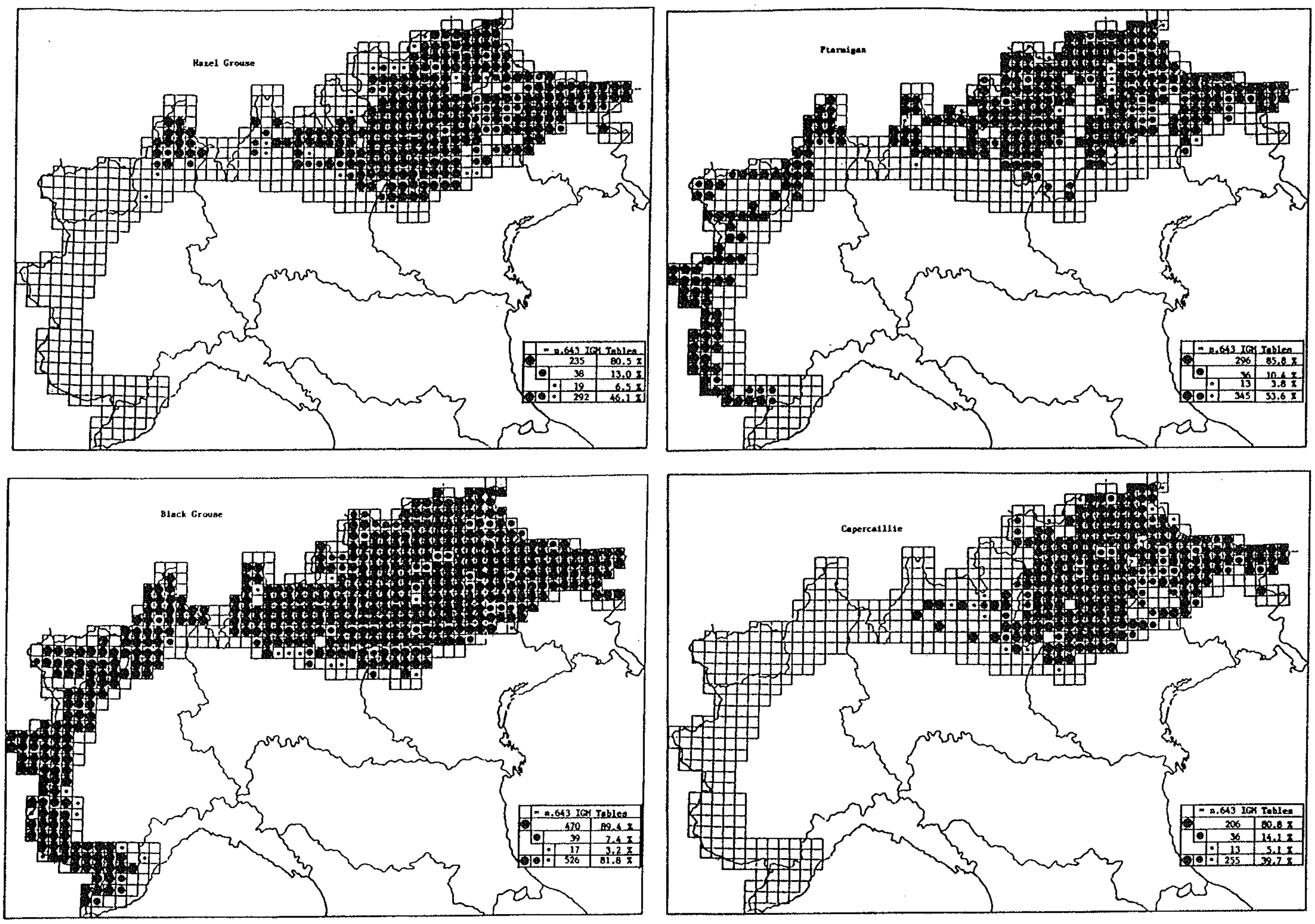

Fig. 1. Nesting areas of Hazel Grouse, Ptarmigan, Black Grouse and Capercaillie. Nesting: 'Certain' (large dots); 'Probable' (medium dots); 'Possible' (small dots).

Results and discussion

Ptarmigan *Lagopus mutus* and Black Grouse *Tetrao tetrix* were found throughout the Italian Alps, but Hazel Grouse *Bonasa bonasia* and Capercaillie *Tetrao urogallus* only in the woodlands of the centre-east (Fig. 1).

Compared with a previous study (Brichetti 1982), the areas occupied by the two forest grouse show a slight decline (Hazel Grouse -1.3%, Capercaillie -1.0%), while there has been an increase for the other two species (Ptarmigan +1.7%, Black Grouse +9.2%). These differences could be due to methodological error and there is no evidence of any big change in the geographic distributions since 1982.

Altitudinal data are given in Table 2. All species recur at lower altitudes on a gradient from west to east. The widths of the "preferred altitudinal belt" (resulting from c. 70% of all observations) range from 400 - 600 m for the grouse (Hazel Grouse 1050-1650 m, Ptarmigan 1800-2400 m, Black Grouse 1450-1850 m, Capercaillie 1200-1700 m), while for the Rock Partridge it was 1100 m (1000-2100 m) (Artuso and Paganin 1993). These altitudinal data on bird distribution in the Italian Alps are the first that have been analysed from such a large data base.

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The distribution and status of Caucasian Black Grouse in north-eastern Turkey

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Introduction

The Caucasian Black Grouse *Tetrao mlokosiewiczi* is very limited in its distribution, being almost entirely restricted to the mountains of Georgia and Armenia (Cramp and Simmons 1980). Two outlying populations occur, one in the mountains of northern Iran, where birds were first seen in 1975 (Scott 1976), and one in the Black Sea coastal mountains of north-eastern Turkey. The Kaçkar mountains, which form the core of the Black Sea range, are now recognised as an Important Bird Area for Europe, partly because of the Caucasian Black Grouse population (Grimmett and Jones 1989). Birds were not regularly recorded in Turkey until the mid 1980s, prior to when there had been only four recorded sightings in north-eastern Turkey (Radde 1884 quoted in Kumerloeve 1967, Kumerloeve 1961, Beaman et al. 1975, Beaman 1986). Since 1980, the vast majority of records of Black Grouse in Turkey have come from a single site, the village of Sivrikaya, which is found near the centre of the Black Sea range. This pattern of sightings is the result of Sivrikaya's relative accessibility and its consequent popularity with bird watchers. However, large areas of upland potentially suitable for Black Grouse exist elsewhere in the region which have not been adequately surveyed.

Caucasian Black Grouse are listed as near-threatened (Collar and Andrew 1988), and Mountford (1988) considers this species to be a candidate for the next edition of the Red Data Book list of endangered species. This designation was based on a combination of the species' limited known range with insufficient knowledge of its true status within that range. Our study aimed to determine more precisely the status and distribution of Caucasian Black Grouse in the mountains of north-eastern Turkey, and to gather information on possible threats to the birds in this area. Data on the behaviour and habitat preferences of Caucasian Black Grouse were also collected, aiming to identify the factors which may be important in determining the birds' distribution.

Methods

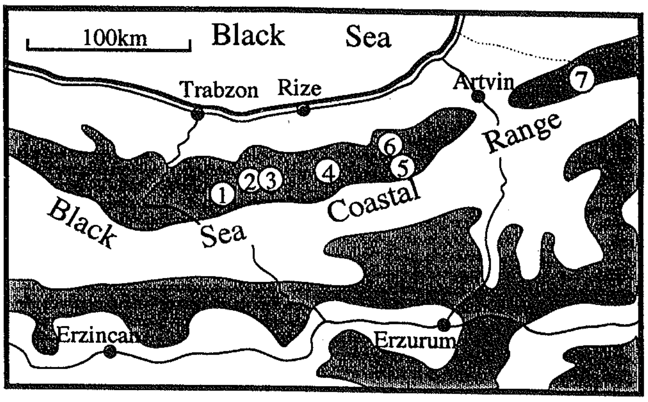

Fig. 1. Map of north-eastern Turkey, showing the locations of sites surveyed for Caucasian Black Grouse:
1) Ablaryas; 2) Yaylaönü; 3) Pladimezraasi; 4) Sivrikaya; 5) Kaçkar Mountains, south; 6) Kaçkar Mountains, north; 7) Balci.
Shaded regions represent land over 2000 m.

Seven sites in the Black Sea coastal mountains of north-eastern Turkey were visited during the breeding season, between 7 May and 30 June, 1993 (Fig. 1). The aim was to cover as wide an area as possible within the breeding season, and sites were therefore chosen firstly to be well spread across the area of suitable altitude (1500 - 3000 m, Cramp and Simmons 1980), and secondly to be readily accessible. Hillsides at each site were observed by telescope from facing slopes on at least two occasions, concentrating on the three-hour periods following dawn and preceding dusk. Grove et al. (1988) found that counts of the numbers of lekking male Black Grouse *Tetrao tetrix* in Wales gave a good index of the total population in an area, and this method of estimation was therefore followed in this study. The peak count of male grouse on each hillside was recorded, together with a number of physical and habitat variables; the maximum altitude, altitudinal range, aspect and incline of each slope were calculated from detailed contour maps, while visual estimates were made of the percentage covers of snow, rock, grass, scrub and forest.

Results

Grouse were found at all the sites visited except one (Table 1). The westernmost record for Black Grouse was previously at Sivrikaya (Site 4, Fig. 1), and this study has therefore extended the known range of Caucasian Black

Table 1. Numbers of hillsides surveyed and the numbers of leks and male Caucasian Black Grouse recorded at each survey site.

Site		No. hillsides surveyed	No. with leks	Total males
1)	Ablaryas	15	6	38
2)	Yaylaönü	5	2	9
3)	Pladimeraasi	8	4	5
4)	Sivrikaya	21	12	60
5)	Kaçkar south	13	8	23
6)	Kaçkar north	3	1	3
7)	Balci	5	0	0
Total		70	33	138

Grouse in north-eastern Turkey approximately 70 km westward.

Kaçkar North was visited after lekking had ceased, making conclusions about the abundance of grouse here unreliable. These hillsides were therefore excluded from the analysis of habitat preferences, the results of which are shown in Table 2 and Fig. 2. Grouse showed significant preferences for hillsides with higher snow and scrub covers and a roughly northerly aspect, but no preferences for any other physical or habitat characteristics. The abundances of snow and scrub were both significantly higher on north-facing hillsides than on other aspects (quadratic regressions, snow cover: $r^2 = 0.4$, $n = 67$, $p < 0.0001$; scrub cover: $r^2 = 0.2$, $n = 67$, $p < 0.003$).

Lekking was in progress at the start of the study on 7 May and had apparently finished by mid June. During this period, some males were present on the lek throughout the day, but peak activity occurred in the three-hour periods after sunrise and before sunset. Presumed territories were held by males on areas of mixed snow and grass a short distance above the tree line, and all birds (male and female) seen leaving leks flew or walked to areas of scrub immediately below the lek or on an adjacent hillside.

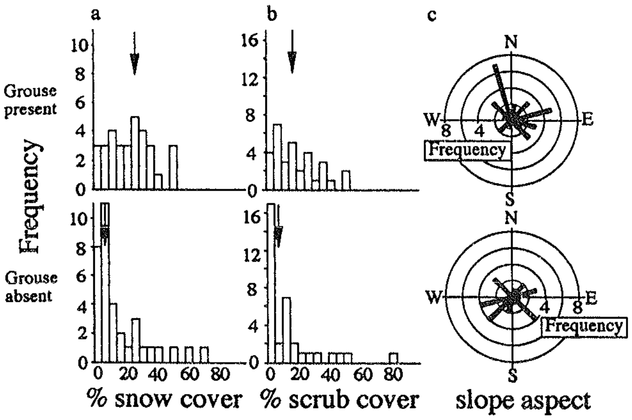

Fig. 2. Comparisons of the characteristics of hillsides with (top row) and without (bottom row) records of Caucasian Black Grouse leks: a) the relationship between snow cover and the presence of leks; b) the relationship between scrub cover and the presence of leks (arrows indicate medians); and c) the relationship of slope aspect and the presence of leks (see Table 2 for statistics).

Table 2. Tests for significant differences between habitat characteristics of hillsides with (n = 32) and without (n = 35) observations of Black Grouse. (NS = non-significant. The test statistic for aspect is Watson's U^2 for circular distributions (critical $U^2_{(0.05)} = 0.185$) and Mann-Whitney U (critical $U_{(0.05)} = 715$) for all other variables. The directions of significant differences are shown in Fig. 2.).

Habitat variable	Test statistic	p
Aspect	0.211	0.025
Maximum altitude	357	NS
Altitudinal range	350	NS
Incline	345	NS
Area	339	NS
Snow	754	0.01
Rock	642	NS
Grass	649	NS
Scrub	760	0.01
Forest	651	NS

Discussion

The discovery in this study of significant numbers of Caucasian Black Grouse, both in and outside their previously recorded range, suggests that the Turkish population of the species is not in immediate danger. Ideally, survey sites should have been selected randomly, and because considerations of accessibility prevented this, the conclusions of this survey regarding the general abundance of Black Grouse should be extrapolated only cautiously to areas which were not visited. It is nonetheless encouraging that Black Grouse were generally found to be well distributed and reasonably abundant.

As well as other parts of the range, two of the sites visited in this study deserve further attention. These are Balci (Site 7, Fig. 1) and north Kaçkar (Site 6, Fig. 1). Balci received much less survey effort than other sites due to illness, and although the area of alpine zone in the region was somewhat restricted and no grouse were recorded there, both the occurrence of extensive apparently suitable habitat and the reports of local people suggested that Black Grouse are present in the area. North Kaçkar was surveyed late in the season when lekking had ceased, and the number of birds seen there does not therefore reflect their true abundance. Again, a large amount of apparently suitable habitat was noted, and it seems likely that the area holds a substantial population of Black Grouse.

The interrelation of the three habitat factors preferred by grouse (high snow cover, high scrub cover and northerly aspect) may be correlated with a slower thaw on north-facing hillsides and the occurrence there of favoured rhododendron spp. (the most common shrubs in the area). Although male grouse clearly require open areas on which to display, the lack of preference for open grass and the observation that birds leaving leks always entered scrub both strongly suggest that grouse usually selected hillsides with higher scrub cover, and that the correlations with snow cover and aspect are incidental. This is further supported by the few records of nests which exist. During this study an abandoned nest was discovered, and Temple-Lang and Cocker (1991) report the discovery of a nest in use, both nests being found in dense rhododendron scrub. It may be concluded that scrub is an important habitat for Caucasian Black Grouse in the breeding season.

Caucasian Black Grouse are fully protected by law in Turkey, although it is clear that a certain amount of hunting still occurs. The extent of this hunting is extremely difficult to assess, however, as a result of its covert and unregulated nature. In the past, hunting was carried out entirely by local villagers, probably at low levels since many areas were inaccessible, and interviews with villagers suggest that Black Grouse are not a highly favoured quarry species. Increasingly, hunting pressure now comes from professional and amateur hunting clubs based in the cities, which are now potentially able to have a large impact as result of improved access by road to alpine areas. Although there is no evidence for excessive hunting at present, more accurate information on the true extent of hunting is required before firm conclusions can be drawn.

Given the apparent requirement of Caucasian Black Grouse for scrub, loss of this habitat is likely to be a major threat to the population. In fact, the scrub habitat is probably not in great danger at present, but changing patterns of land use in the area may lead either to a reduction or an increase in the abundance of scrub, for the following reasons. Trees are cut for fuel and timber in the vicinity of high altitude summer villages, leading to a reduction in forest cover near the tree line. This often results in a mixture of scrub and pasture which may benefit Black Grouse. In very densely populated areas, however, even this scrub may disappear due to cutting of firewood and bedding for livestock, associated with intense grazing which prevents regeneration. The size of the grouse population would therefore appear to depend on a delicate balance of human land use. Discussions with villagers and officials of the Forestry Department suggested that the human populations of high altitude summer villages are presently decreasing as the rural economy declines and more people find work in urban areas. In the short term, at least, this is probably good news for the grouse, as it should allow the regeneration of large areas of scrub previously grazed heavily. It should be noted, however, that if, in the long term, depopulation takes place to the extent that there is widespread regeneration of forest at its upper limits, this could in theory lead to a reduction in the grouse population. Although Caucasian Black Grouse are apparently not critically endangered in Turkey at present, it is recommended that they retain their near-threatened status, at least until reliable information is available on human population trends and their implications for upland habitats.

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Summary

A survey of Caucasian Black Grouse was carried out in the mountains of north-eastern Turkey. Information was collected on their distribution, abundance and habitat preferences, and on the nature and severity of threats facing the population. Black Grouse were found to be more widespread than previously recorded and were abundant in some of the sites visited. A preference for areas with high scrub cover was demonstrated, and it is suggested that this habitat is potentially vulnerable. Although Black Grouse are hunted in the region to an uncertain extent, the population is probably not severely threatened by this activity at present. Despite the apparent health of the Black Grouse population in Turkey at present, in view of the uncertainties surrounding future patterns of land use in the region and their effects on the preferred habitat of the grouse, it is recommended that Caucasian Black Grouse in Turkey retain their current status as near-threatened.

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Chemical characteristics of some Black Grouse foods in September in the eastern Italian Alps

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Introduction

In all habitats, Black Grouse *Tetrao tetrix* show selective feeding behaviour, not only in terms of plant species eaten but also the various parts of the plants (Chapuis et al. 1986). Of the factors considered to influence the selection process, various authors (De Franceschi 1978, 1981, Pauli 1978, Marti 1985) have indicated the importance of the concentration of nutrient substances and digestibility.

The aim of this work was to provide some preliminary information about the chemical characteristics of several foods selected by *Tetrao tetrix* in the Italian Alps. Particular attention has been given to protein and the composition of cell walls and cell contents.

The plant cell wall is a matrix of structural polysaccharides, lignins and phenolics, with a complex series of linkages. Lignin is considered the main factor limiting digestibility in forages (Van Soest 1983). The phenolic composition of cell walls is an expression of the cross-linkage of matrix components which could help in understanding the mechanisms by which cell wall chemistry limits fibre digestion (Jung and Casler 1991).

Location and material

The foods were sampled in September 1993 near Collinetta on the Coglians Mountain in the central Carnic Alps. Sites were sampled at 1500 - 1670 m ASL.

Hand clipping was used to harvest the parts of plants (stems, leaves, buds and berries) that *Tetrao tetrix* eat in September (Table 1), based on observations by de Franceschi (1981).

Methods

Samples were dried at 65°C for 48 h and then milled to pass a 1 mm screen. Foods were analysed for proximate constituents, N*6.25 and ash and fibre fractions (ASPA 1980). Samples were washed five times with 80% ethanol (Theander and Westerlund 1986), and then extracted with 2M NAOH to obtain ester-linked phenolics (Jung and Shalita-Jones 1990). Ether-linked phenolics were extracted from 2M NAOH residues with 4M NAOH at 170°C for 3 h (Iiyama et al. 1990). Extracts were analysed with a Perkin-Elmer Series 10 HLPC with a Supelcosil LC-8 column at 25°C. Eluent was 28% methanol and phenolics were detected at 270 nm.

Results

The organic matter (OM) and N*6.25 content of foods are shown in Table 1. For all foods, the ash component was low. The protein content of green matter was variable and relatively high both in *Vaccinium myrtillus*, which is highly palatable, and in *V. gaultherioides*, which is not generally eaten. The berries had a N*6.25 concentration lower than their plant green matter.

Cell wall (NDF) and cell wall component concentrations are presented in Table 2. Among *Vaccinium* green matter, *V. uliginosum* had the highest content of NDF and lignin (ADL). These species also had the highest level of hemicellulose, which was generally low in the analysed food. Of the *Rhododendrons, R. hirsutum* had the highest cell wall content. The berries had lower cell wall contents than their plant green matter.

The concentration of phenolic components is reported in Tables 3 and 4. As the berries had only a modest NDF level, they were not analysed for phenolics. In the *Vaccinium* green

Table 1. Percentages (DM basis) and composition (% DM) of some foods in the September diet of *Tetrao tetrix* in the eastern Italian Alps.

Species	Plant part	Percentage in September diet	Organic matter	N*6.25
Vaccinium myrtillus	green matter	25.2	95.3	10.9
V. vitis idaea	"	0.5	96.1	6.9
V. gaultherioides	"	1.1	96.0	11.5
Rhododendron hirsutum	"	1.1	95.2	8.8
R. ferrugineum	"	0.6	97.1	10.1
R. ferrugineum	buds	2.9	97.0	8.9
V. myrtillus	berries	27.7	97.8	7.1
V. vitis-idaea	berries	3.8	97.7	6.1

Table 2. Cell wall constituents (% DM) of some foods in the September diet of *Tetrao tetrix* in the eastern Italian Alps.

Species	Plant part	NDF	Hemicellulose	ADF	Cellulose	ADL
Vaccinium myrtillus	green matter	35.0	5.3	29.7	16.5	13.2
V. vitis-idaea	”	33.6	2.0	31.6	18.1	13.5
V. gaultherioides	”	41.4	7.6	33.5	16.9	16.6
Rhododendron hirsitum	”	48.4	4.9	43.5	19.4	24.1
R. ferrugineum	”	28.9	3.5	25.4	12.1	13.3
R. ferrugineum	buds	39.7	1.3	38.4	16.1	22.3
V. myrtillus	berries	22.5	5.1	17.4	10.0	7.4
V. vitis-idaea	berries	22.3	9.0	13.3	5.8	7.5

Table 3. Esterified phenolic compounds (mg/100 g NDF) of some foods in the September diet of *Tetrao tetrix* in the eastern Italian Alps.

Species	Plant part	PHBA	VANA	SYA	VANL	SYAL	PCA	FA	Total phenolics
Vaccinium myrtillus	green matter	6.9	10.7	0.0	8.1	0.0	19.1	5.5	50.3
V. vitis-idaea	”	4.6	8.9	0.0	4.6	0.0	20.8	10.3	49.2
V. gaultherioides	”	16.0	15.9	0.0	18.7	0.0	19.9	26.3	96.7
Rhododendron hirsitum	”	5.5	4.3	0.0	4.7	0.0	28.9	20.8	64.3
R. ferrugineum	“	9.0	13.9	0.0	2.3	0.0	32.2	16.2	73.7
R. ferrugineum	buds	5.0	3.9	0.0	4.5	0.0	15.3	14.9	43.6

PHBA: *p*-hydroxybenzoic acid; VANA: vanillic acid; SYA: syringic acid; VANL: vanillin; SYAL: syringaldehyde; PCA: *p*-coumaric acid; FA: ferulic acid.

Table 4. Etherified phenolic compounds (mg/100 g NDF) of some foods in the September diet of *Tetrao tetrix* in the eastern Italian Alps.

Species	Plant parts	PHBA	VANA	SYA	VANL	SYAL	PCA	FA	Total phenolics
Vaccinium myrtillus	green matter	18	216	0	680	511	107	114	1646
V. vitis-idaea	”	76	171	345	134	367	75	96	1264
V. gaultherioides	”	8	40	0	251	0	285	59	643
Rhododendron hirsitum	”	55	91	0	254	92	70	50	612
R. ferrugineum	”	0	38	0	261	148	58	51	556
R. ferrugineum	buds	12	132	0	505	377	34	97	1157

PHBA: *p*-hydroxybenzoic acid; VANA: vanillic acid; SYA: syringic acid; VANL: vanillin; SYAL: syringaldehyde; PCA: *p*-coumaric acid; FA: ferulic acid.

matter, *V. gaultherioides* had the highest content of total esterified phenolics. *p*-Coumaric acid (PCA) and ferulic acid (FA) were the principal components in all foods.

The etherified phenolics had an opposite pattern to the esters. Phenolics were high in *V. myrtillus*, *V. vitis-idaea* and *R. ferrugineum* buds. Vanillin (VANL) and syringaldehyde (SYAL) were the major components of the etherified phenolics in *V. myrtillus* and *Rhododendron*. In *V. vitis-idaea*, there was also a high proportion of syringic acid (SYA), whilst PCA had a high concentration in *V. gaultherioides*, from 2 to 8 times higher than that observed in the other foods.

Discussion

Numerous authors state that the *Vaccinium* species are the most important components in the autumn food of Black Grouse (Bernard 1979, Pauli 1978). In the central Carnic Alps (de Franceschi 1981), *Vaccinium myrtillus* was the most abundant species in the crops and gizzards of Black Grouse. Although only a small number of analyses have been performed so far, on the basis of these it appears that the protein and cell wall content are no more important than other nutrients in determining the selection of the green matter of berries of *V. myrtillus*.

However, in any case it would appear to be worthwhile to examine more closely the high levels of NDF and ADL in *V.gaultherioides* which, in comparison with the other black berries, is the least palatable species in the autumn diet. The NDF and ADL are associated with the highest esterified phenolics content, and these have the greatest probability of interfering with the digestive processes. PCA and FA, in particular, made bridges between hemicellulose chains and hemicellulose and lignin (Yamamoto et al. 1989, Jung and Deetz 1993).

Finally, of the etherified phenolics, it is worth mentioning the high concentrations of vanillin in *V. myrtillus*.

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Ecological studies of Hazel Grouse at Changbai Mountains using radio-telemetry

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Introduction

Formerly, Hazel Grouse *Bonasa bonasia* were widely distributed and abundant in north-east China and were offered to the Qing Imperial palace as tributes, known as 'flying dragons'. Some people in north-east China also called them 'ginseng birds' because ginseng *Panax ginseng* was often found in association with Hazel Grouse. In recent years, due to the reduced size of preferred habitat and to overhunting, numbers of Hazel Grouse have been reduced dramatically, and at present, the species is listed as a second-rank protected bird in China.

Radio-telemetry work was conducted in the Changbai Mountains at 700 - 900 m ASL in 1992-93.

Study area

The Changbai Mountains are a series of parallel mountain ranges running north-east/south-east in north-east China. The climate was temperate continental mountain affected by monsoon, and annual mean temperatures varied between -7.3 - 4.9°C, but up to 16 - 20°C in July and down to -22 - minus 16°C in January.

The vertical zonation of forest on the north slope of the Changbai Mountain was very marked, changing from mixed coniferous/deciduous forest at 500 m, through coniferous forest to Ermans birch *Betula ermanii* forest at 2000 m.

Korean pine *Pinus koraiensis* was the dominant species in mixed coniferous/deciduous forest up to 1100 m, with David's poplar *Populus davidiana* and Asian white birch *Betula platyphyla* on the drier sites, and with a rich mixture of temperate broad-leaved species such as Amur lime *Tilia amurense,* mono maple *Acer mono*, Manchurian ash *Fraxinus mandshurica*, Japanese elm *Ulmus propinqua* and Manchurian walnut *Juglans mandshurica* on moister sites.

Coniferous forest at 1100 - 1700 m contained pure or mixed stands of Olga Bay larch *Larix olgensis*, littleseed spruce *Picea jezonensis*, Khingan fir *Abies nephrolepis* and Scots pine *Pinus sylvestris.*

Ermans birch forest at 1700 - 2000 m was dominated by Ermans birch, with occasional dwarf Siberian pine *Pinus pumila*, Manchurian alder *Alnus mandshurica* and showy mountain ash *Sorbus decora.*

After a long period of felling, second-growth forest has became abundant in this area, dominated by David's poplar and Asian white birch mixed with some conifers, such as littleseed spruce.

Methods

We counted Hazel Grouse in spring and autumn from responses to calls imitated by whistles. Line transects and plot estimates were also used in this study. Line transects were walked in spring and autumn from 1973 - 1992, with our work from 1989 - 1992. In three kinds of forest at 800 - 1900 m, we walked at 3 km/hour imitating the call of grouse by whistles. Plots were set up in different habitats. Plot counts were done in spring from 0530 - 0930 h, when we walked through the plots whistling every 150 m, repeating the call at 15 sec intervals. All the plots were counted 7 - 8 times on different days and positions of birds responding or seen were mapped.

Eight grouse, captured by nets or at nests, were fitted with backpack transmitters weighing 12 - 16 g (less than 4% of body weight) made by ourselves (Kenward 1987). Radio-tagged birds were located with a receiver (Model CE-12) and a hand-held yagi antenna, two to four times daily from short distances (usually 20 - 500 m). Females were monitored frequently from 0700 to 1830 h when incubating. Locations were determined by taking compass bearings and pacing to known reference points.

Home range sizes were calculated by the minimum convex polygon (MCP) method (Mohr 1947).

Results and discussion

Population densities in different habitats

Numbers of Hazel Grouse were estimated in plots in four different habitats in spring in both 1991 and 1992 (Table 1). Presumably because second-growth forest provided grouse with much food and enough cover, the population density in

Table 1. Population densities of Hazel Grouse in different habitats in spring 1991 and 1992.

Forest type	Altitude (m)	Plot area (km^2)	Density (birds/km^2)
Mixed coniferous / deciduous	900	0.75	5.3±1.4
Coniferous	1500	0.30	3.4±1.2
Ermans birch	1750	0.45	2.2±1.6
Second-growth	800	0.65	26.1±2.3

Table 2. Rates of encounters with Hazel Grouse on line transects in three forests in 1973-92.

Year	Encounter rates of Hazel Grouse (nos. recorded per hour)				
	Second-growth		Mixed coniferous / deciduous		Coniferous
	Spring	Autumn	Spring	Autumn	Spring
1973-4	2.05		0.89		0.40
1976		1.39(33)*		1.07(29)	
1977		1.06(52)		0.86(44)	
1978		0.93(42)		1.71(14)	
1982		0.52(21)		0.45(11)	
1983		0.30(27)		0.55(31)	
1984		0.38(37)		0.42(72)	
1989	0.80(13)		0.31(7)		
1990-91	0.017(59)	0.27(44.5)	0.063(48)	0.18(28)	0.15(21)
1992	0.60(76)	0.43(7)	0.36(20)	0.25(18)	

* number of hours spent walking.

second-growth forest was much higher than that in the other three habitats, where food and cover were both less abundant, especially in the Ermans birch forest. The habitat in coniferous forest was similar to that in north Europe, where the density was between 0.6 - 13.5 males/100 ha (Swenson 1991a). Though we used different methods, our estimate of c. 1.7 males/100 ha was similar to the data from Sweden and Poland.

Population dynamics

The results in Table 2 and Fig. 1 suggest that relative densities of Hazel Grouse have decreased sharply over the past 20 years, in both second-growth and virgin forest. Encounter rates dropped from over 2 birds per hour in spring in 1973 - 74 to 0.6 - 0.8 in 1992 and 1989 and to much less in 1990 - 91. The most important reason was overhunting from October to February in every year. Because these grouse can be lured by whistle, they are easily hunted. There are more than 50,000 people in Erdaobaihe town, near our study area, and many of them own guns. Although the Hazel Grouse is listed as a second-rank protected bird in China, management measures fall short of the requirements of conservation.

Home range of males

The monthly home range areas of two males were between 10.7 and 152.8 ha in April -August (Table 3). The home range area of bird A was larger than that of bird B, perhaps because B's wing was slightly wounded during catching. As a result, B could not fly as well as others. But B still responded well to whistle-calls in May when it was very difficult to see him even though the receiver showed where he was, because he was very alert and could conceal himself silently in the shrubs.

The home range size of bird A decreased in July and early August (Fig. 2), as found for Hazel Grouse in Sweden (Swenson 1991b) and Ruffed Grouse *Bonasa umbellus* in America (Gullion and Martinson 1989). Bird A left his mating territory at the end of June and moved into a relatively fixed area, where his favourite foods, the fruits of honeysuckle *Lonicera edulis*, oriental strawberry *Fragaria orientalis* and bloodwort *Sambucus williamsii* and insects such as grasshoppers were very abundant. His activity centres (Fig. 2) coincided with shrub areas. After mid-August, the home range of bird A increased when the fruits of honeysuckle and strawberry ripened.

Home range of females during incubation

Four female grouse were caught at their nests. In late incubation, they (C, D, E, F) left their nests to feed once daily at noon. In rather few days of observations their feeding range was 0.34 - 0.63 ha (Table 4). Bird C, which lost her clutch and was released far from her nest, did not re-nest and had a much larger home range area of 12.2 ha.

Table 3. Monthly home range areas (ha) of male Hazel Grouse at Changbai in 1993

Bird	Telemetry period				
(Male)	April	May	June	July	August
A	28.0	29.4	152.8	18.6	58.2
B		10.7	25.5		

Brood development

Three hens succeeded in hatching, but F was killed by a predator on 13 June and E lost her chicks on about 22 June. After her 11 chicks hatched, D led the brood for 40 days (27 May to 6 June). Bird D and her brood moved farthest, 1.7 km, but E did not show this pattern. E led her brood in an area of 15.9 ha only 250 m from her nest (Table 5).

After wandering with the chicks for 40 days, D stayed in a fixed area near ginseng farms and reared 4 chicks. Home ranges of bird D with her chicks in July and August were 11.0 and 25.5 ha. When her chicks dispersed in mid-August, D returned to her nest area. After losing her five chicks in late June, E moved to an area near her nest, with home range areas of 5.3 and 7.6 ha in July and August.

According to our tracked grouse, forest roads served as boundaries of their home ranges. Although the roads were only 8 - 10 m wide, the grouse did not cross, perhaps to avoid additional dangers. However, grouse without transmitters were sometimes seen flying across the roads and some sand-bathed on road edges.

Sand-bath behaviour

During summer, Hazel Grouse sand-bathed often, perhaps to clean their plumage or discourage parasites. There were some fixed "sand-bathing sites" in home ranges. In virgin forests, the grouse sometimes sand-bathed among the roots of wind-blown trees. But in second-growth forests, there were few wind-thrown trees, so sites for sand-bathing were rare. From our radio-tracking results, bird D and her chicks used ginseng farms for sand-bathing sites. Because ginseng cannot stand rain, crops were protected by plastic sheds on the ginseng farms and here soft soil was suitable for sand-bathing. The grouse were also seen to sand-bathe on the forest roads at midday, when there were few automobiles.

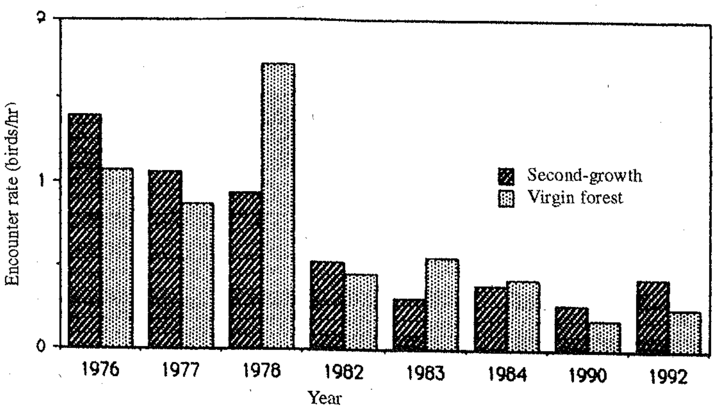

Fig. 1. Encounter rates (birds/hr) of Hazel Grouse at Changbai Mountains during 1976 to 1992. The relative density decreased sharply after 1978 in both second-growth and virgin forest.

Roosting behaviour

Hazel Grouse sometimes spent winter nights in snow-burrows. When the snow was not thick enough for burrowing, they roosted in conifer trees which offered concealment and warmth. In the night, the grouse were still alert to enemies. When we arrived at a conifer tree in which a grouse roosted, it might fly off over the forest and go far away when we prepared to catch it.

Mating behaviour

Males were highly sensitive to the calls of others. A female grouse in a cage was put in the forest to study the response of males. Solitary males showed sensitive reactions to the calls of our female. Sometimes they flew to approach her and stood on the cage. But paired males were not as responsive as unmated birds.

Table 4. Home range areas of three females during incubation in 1993

Bird	Nest altitude (m)	Clutch size	Incubation period / hatching date	Nos. chicks hatched	Daily range area (ha)
C	730	10	failed		
D	710	12	2-27 May	11	0.34 (4)*
E	760	9	?-29 May	8	0.47 (1)
F	830	11	?-31 May	5	0.63 (2)

* Nos. of days of radio telemetry observations

Table 5. Distances (m) moved by two females with broods at Changbai in 1993

		Time after hatching (days)									
		0.5	1	3	9	12	18	20	25	28	31
Distance (m)	)Bird D	85	180	600	490	870	730	720	1010	1290	1700
	)Bird E		100	140	170	250	180				

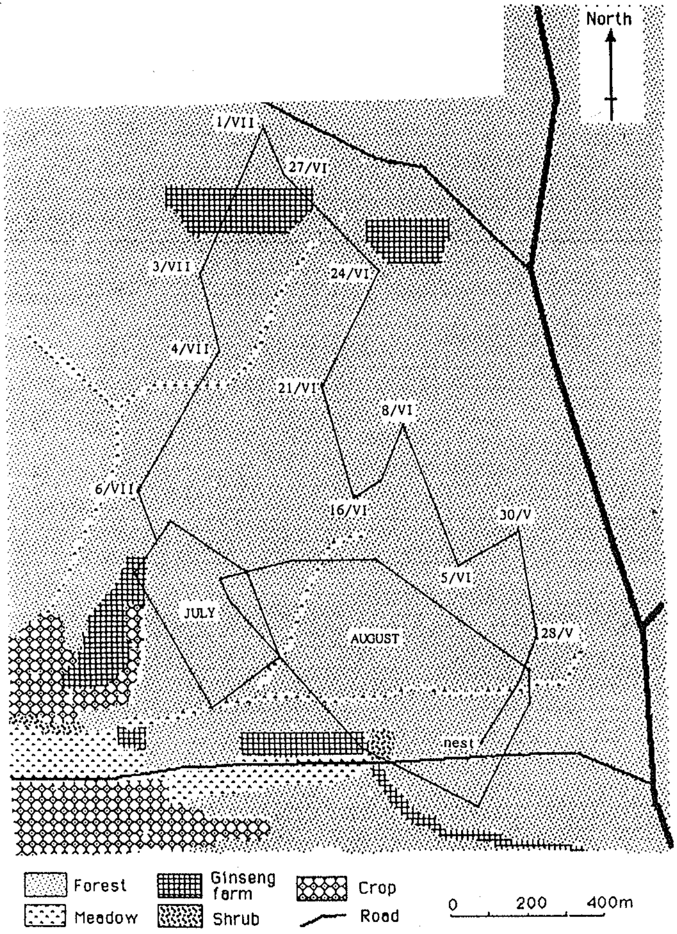

Fig. 2. Home range map of D from May - August. After hen 11 chicks hatched, D led her brood for days (27 May - 6 July).

Natural enemies

In spring and summer, raptors and mammals killed adult grouse. Snakes, Eurasian jays *Garrulus glandarius* and chipmunks took eggs (Zhao 1977). In our study, two radio-tracked grouse were killed by mammals and one was killed by a raptor: the transmitter was found on a branch of an epinette tree at 15 m.

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Summary

We studied Hazel Grouse in the field at Changbai Mountains in Jilin Province from 1989 -1993. The spring population density varied from 2.2 - 26.1 birds/km^2 in different habitats in 1991 - 92, having decreased sharply in the past 20 years. Eight Hazel Grouse (3 males and 5 females) were studied during April to August. In spring, monthly home range areas of males varied from 10.7 to 152.8 ha, bigger than those of females. In July and early August, a male grouse moved into a small area (18.6 ha), where deep blue honeysuckle and oriental strawberry were abundant. Home ranges of females during late incubation were 0.34 - 0.63 ha. One female led her brood up to 1.7 km from her nest over a 40-day period. When the chicks left her in mid-August, the hen went back to her mating territory. Sand-bathing was an important activity in summer, particularly on ginseng farms. Roosting and mating behaviour were also studied in spring and winter.

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Habitat selection and breeding success of Hazel Grouse at Changmai Mountain in 1974-92

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Introduction

Habitat selection and breeding success of the Hazel Grouse *Bonasa bonasia* were studied mainly in the Changbai Mountain area from 1974 to 1992. Changbai Mountain (up to 2691 m ASL) is situated in the east of Jilin Province (41° 10' - 44° 50'N, 125° 20' - 130° 40'E). Its south-eastern part forms the border between China and the People's Democratic Republic of Korea. From the foot of the mountain to the main peak, the vegetation can be divided into five vertical plant zones, as follows.

a. Below 600 m - broadleaved forest, on basalt and mainly undulating; climate, temperate mountainous broadleaved forest type, average annual temperature above 3°C, average temperature -15°C in January and above 22°C in July, frost-free period c. 100 d. Main tree species: *Quercus mongolica, Populus davidiana, P. simonii, P. ussuriensis, Alnus mandshurica, Betula platyphylla, Tilia mandshurica, Acer ginnala, Ulmus propinqua.*

b. 600 - 1100 m - mixed conifer/broadleaved forest zone, main tree species: *Pinus koraiensis, Larix olgensis, Juglans mandshurica, Ulmus japonica, Ulmus lacinata, Ulmus propingqua, Tilia amurensis, Quercus dentata, Fraxinus mandshurica, Acer mono, Populus ussuriensis, P. davidiana, Betula platyphylla,* and *Betula costata.*

c. 1100 - 1700 m - conifer forest on a slight slope zone connecting the high peaks of Changbai Mountain; climate, temperate mountainous coniferous type, average annual temperature -3°C, hottest month July with average temperature 20°C, frost-free period 90 d. Main tree species: *Pinus koraiensis, Larix olgensis, Picea jezoensis, P. koraitensis,* and *Abies nephrolepis* with sparse *Betula ermanii, B. platyphylla, Alnus sibirica* and *Acer barbinerves.*

d. 1700 - 2100 m - *Betula ermanii* forest zone. Main tree species: *Betula ermanii.*

e. 2100-2691 m - mountainous tundra zone. The climate is temperate mountain tundra type, with average annual temperature -5°C. In the coldest month, the average temperature is c. -25°C in January and no more than 10°C in the warmest month in August; frost-free period 60 d with snow cover for 250 d every year. No trees. Vegetation is mainly small shrubs 10-20 cm high, lichens and mosses such as *Dryas octopetala, Vaccinium vitis-idaea, V. uliginosum, Rhododendron aureum, Phyllodoce caerulea, Rhacomitrium lanuginosum, Rh. canescens, Cladonia rangiferina, Cl. alpestris.*

Hazel Grouse were counted using route transects, walking along defined survey routes at 2-3 km/h in different types of habitat while imitating the call of Hazel Grouse (Zhao 1977), and recording encounters and the response of birds to the imitated song. Counts were repeated in different months, years, altitudes and forest types, on average 5 times every month over at least 2 h every day, and 2-3 months every year.

Table 1. Habitats used by Hazel Grouse at Changbai mountain in summer and autumn, 1974-92.

Habitat	Summer			Autumn		
	Nos. of counts	Nos. of birds recorded	Encounter frequency	Nos. of counts	Nos. of birds recorded	Encounter frequency
Forest type						
a) Native						
Broadleaved forests	134	35	0.26	230	110	0.48
Conifer forests	158	50	0.32	252	140	0.56
Mixed forests	195	89	0.46	252	155	0.62
Regenerating poplar/birch	129	32	0.25	260	112	0.43
Erman's birch forests	24	3	0.13	10	1	0.10
Thickets	44	2	0.05	34	8	0.23
b) Plantations						
Monoculture pine forests	15	0	0	14	0	0
Monoculture poplar forests	17	0	0	14	0	0
Mixed forests	15	0	0	12	0	0

The habitat was analysed by forest type, abundance of food resource, elevation and class of forest. Habitat preference was assessed in varied habitat types by comparing estimates of population density. Breeding success was studied by finding nests, recording clutch size, numbers of eggs hatched and numbers fledged from every nest. Breeding was defined as successful when at least one young left the nest.

Results

The distribution of the Hazel Grouse differed seasonally and annually as well as with habitat type. Hazel Grouse were not recorded in plantations (Table 1). They were mainly found in regenerating poplar/birch forests in the non-breeding season, but not in the breeding season.

In summer and autumn, the most preferred habitat was natural mixed conifer/broadleaf with single species coniferous forests and broadleaved forests next. Ranking of habitat preference in the breeding season showed first, mixed forests of conifers and broadleaved species, second, coniferous forests, third, broadleaved forest, fourth, regenerating forests and finally, thicket. In the non-breeding season, the ranking was first, naturally regenerating poplar-birch, second, mixed forests of conifers and broadleaf species, third, coniferous forests, fourth, broadleaf forests, and finally, thickets.

Habitat utilization also differed with altitude in Changbai Mountain. At 800 - 1500 m, the density of Hazel Grouse was highest and they occurred throughout the year. At 1500 - 2100 m, both population density and time of residence gradually decreased, with birds often occurring only in the breeding season. Above 2100 m, there were no Hazel Grouse. Although Hazel Grouse were also scarce below 800 m, they occurred there throughout the year.

Habitat preference of Hazel Grouse in the breeding season appeared to depend mainly on food, shelter and availability of suitable nest sites. There were abundant food resources, good shelter and suitable nest sites for Hazel Grouse in the mixed virgin forests of conifers and broadleaved species and in virgin conifer forests in Changbai Mountain area. Among the 48 species which have been recorded as Hazel Grouse foods (Zhao 1977), almost all can be found easily in both mixed forests and coniferous forests, and they are rather abundant. However, when the food resources and shelter condition were better and the forest layering greater, the rate of breeding success was higher. However, in winter, habitat preference was mainly correlated with food availability and daylight reaching the forest floor (Table 4).

According to Zhao (1977), the winter diet of Hazel Grouse consists mainly of buds and catkins of poplar (*Populus davidiana, P. ussuriensis*), birch (*Betula platyphylla, B. costata*) and alder (*Alnus japonica*). These food resources were plentiful in the naturally regeneratiang poplar/birch forests in Changbai Mountain where Hazel Grouse were found in winter. Both encounter rate and population density were higher where food was apparently plentiful.

Discussion

Hazel Grouse showed a strong preference for certain forest characteristics. At Changbai Mountain, they preferred to inhabit virgin mixed forests and virgin conifer forests in summer (Table 1). A preference for these two types of habitats seemed to depend less on the abundant food resources than on good shelter quality. Because the virgin forests in Changbai Mountain were located on the border of China and Korea, there were less human activities there. In addition, the virgin forests in Changbai Mountain provided much high vertical cover and high horizontal cover. Hazel Grouse may prefer spaces under high vertical cover, especially in winter when they mainly forage in tall trees. Sometimes they may roost also in trees but also in snow holes.

Table 2. Habitats used by Hazel Grouse at Changbai mountain in spring and winter, 1974-92

Habitat	Spring			Winter		
	Nos. of counts	Nos. of birds recorded	Encounter frequency	Nos. of counts	Nos. of birds recorded	Encounter frequency
Forest type						
a) Native						
Broadleaved forests	130	42	0.32	745	266	0.36
Conifer forests	123	26	0.21	468	196	0.42
Mixed forests	152	45	0.30	519	274	0.53
Regenerating poplar/birch	122	45	0.37	803	431	0.54
Erman's birch forests	15	0	0	10	0	0
Thickets	60	7	0.12	103	12	0.12
b) Plantations						
Monoculture pine forests	70	0	0	14	1	0.07
Monoculture poplar forests	40	0	0	40	1	0.03
Mixed forests	20	0	0	20	1	0.05

Table 3. Frequency (%) of Hazel Grouse observations by forest type at Changbai mountain in 1974-92

Forest type	Spring	Summer	Autumn	Winter
a) Native	n=132	n=147	n=242	n=212
Broadleaved forests	24.24	17.68	19.87	16.98
Conifer forests	15.90	21.77	23.14	19.81
Mixed forests	22.73	31.29	25.62	25.00
Regenerating poplar/birch	28.03	17.06	17.76	25.47
Erman's birch forests	0	8.84	4.13	
Thickets	9.09	2.40	9.54	5.66
b) Plantations				
Monoculture pine forests	0	0	0	3.30
Monoculture poplar forests	0	0	0	1.41
Mixed forests	0	0	0	2.35

Table 4. Correlation of habitat characteristics and preferences and breeding performance (summer and autumn).

Habitat type	Preference class	Hatching success (%)	Shelter	Food resource	Breeding success (%)
Broadleaved forests	3	19	B	C	70
Conifer forests	2	29	B	A	87
Mixed forests	1	40	B	A	81
Regenerating forests	3	14	C	S	66
Thickets	5	4	0	S	60
Erman's birch forests	5	2	0	S	-

Note: Habitat preference (% of observations) is divided into 6 classes: 1) preference was 50 - 60%, 2) 40 - 50%, 3) 30 - 40%, 4) 20 - 30%, 5) 10 - 20%, 6) 0 - 10%. Hatching and breeding success was at least one young bird leaving the nest. Shelter - B, up to 70% of forest closed; C, 50 - 70% of forest closure; 0, below 50% forest closed. Food - A food abundant (50 species of food plant recorded); C common, 20 - 40 species; S less than 20 species.

Table 5. Correlation between habitat preference, food, daylight reaching the forest floor, and elevation in the non-breeding season.

Habitat type	Elevation (m)	Food resources	Daylight reaching forest floor	Preference class
Broadleaved forest	500-700	C	C	2
Conifer forest	1100-1700	C	B	3
Mixed forest	700-1100	A	C	1
Regenerating poplar/birch	700-1200	A	A	1
Erman's birch forests	1800-2100	L	A	6
Thicket	500-1000	C	C	5

Note: Habitat preference is divided into 6 classes; 1. 50-60%, 2. 40-50%, 3. 30-40%, 4. 20-30%, 5. 10-20%, 6. 0-10% in preference degree. Food - C - common; A - abundant; G - good; L - less; B - bad. Daylight - A, most; C, least.

Several European studies on the winter diet of Hazel Grouse have shown that they have a high preference for alders (Swenson 1993) and birch. Our results on the food of Hazel Grouse in China were similar in that the winter diet consisted mainly of poplar and birch buds and catkins which were dominant and abundant. From this, it seems that poplar and birch may be major factors determining the distribution and population density of Hazel Grouse in winter in China (Table 3). Winter habitat preference may depend on the abundance and distribution of poplar and birch, especially along road edges and stream shores.

Presumably Hazel Grouse take poplar, birch and alder as winter food because they provide nutritious and protein-rich nourishment in winter. Hazel Grouse are also one of the few grouse species which exhibit territoriality in winter (Swenson 1991), and they have been thought to have the most demanding territory requirements because they feed only in their territories and winter food is an important defensive resource (Swenson 1993). However, territorial behaviour by Hazel Grouse is not obvious in winter in China when they often move and forage in small flocks of 3-5 individuals. Perhaps this is correlated with the wide distribution and abundance of poplar and birch in north-east China.

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Summary

Spatial distribution, habitat preference and breeding success of Hazel Grouse have been studied in Changbai Mountain in China. Results show that the habitat preference was different in the breeding season from the rest of the year. Natural mixed forests of coniferous and broad-leaved species were markedly preferred in summer and autumn. Ranking of habitat preference showed mixed forests of coniferous and broad-leaved species > coniferous forests > broad-leaved forests > regenerating forests > thicket in the breeding season. But in the non-breeding season, regenerating forests > broad-leaved forests > mixed forests > coniferous forests > thicket. Habitat preference depended on food, shelter and availability of suitable nest sites. The habitat utilisation rate was correlated with food availability, and shelter quality with breeding success. When the food resource and shelter conditions were better, the breeding success was high. However, in winter, habitat preference was mainly correlated with food availability.

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Workshops

Habitat requirements of Black Grouse

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Introduction

Black Grouse *Tetrao tetrix* are found in a wide variety of habitats throughout their range and probably have the broadest habitat requirements of the three Eurasian forest grouse species. Typically, they are regarded as birds of early stage succession forest, either coniferous or birch *Betula* spp. and forest edge habitats, particularly in boreal zones. Outside the boreal regions, Black Grouse are found in structurally similar habitats comprised of mosaics of moorland or heathland, coniferous plantations, rough grazing fields and meadows (Degn 1973, Ellison 1979, Parr and Watson 1988, Baines 1994). In many of these habitats, their association with woodland is not strong, with preferred tree crown cover 0.3 - 12% (Beichle 1987). Open canopied coniferous woodlands of pine, spruce or larch allow sufficient sunlight to reach the forest floor and create a field layer rich in herbs, bilberry *Vaccinium myrtillus* and rhododendron *Rhododendron ferrugineum* attractive to Black Grouse. Closed canopy woods have no such field layer and tend to be avoided.

By having such a wide range of habitat preferences, identifying particular habitat requirements pertinent to all populations across the species' range is difficult. Black Grouse feed selectively according to the nutritive quality, availability and digestibility of the food items. I suggest that there are three potentially limiting dietary stages for Black Grouse; these are a protein and energy rich food source for females in the pre-laying period, adequate invertebrates preferred by chicks, and a reliable winter food source.

This review attempts to concentrate on similarities over how these requirements are met by different Black Grouse populations. Current knowledge is discussed under the headings of winter food, spring food, breeding requirements and spatial or landscape ecology. Research recommendations aimed at filling gaps in our understanding of the wider requirements of Black Grouse are suggested.

Winter food

Even under severe alpine winter conditions with deep snow over prolonged periods, Black Grouse do not appear to suffer from food shortages (Pauli 1974). However, in the French Alps, the spatio-temporal distributions of Black Grouse and skiers suggests that birds may be excluded from the best wintering areas by disturbance and that, as a consequence, food and foraging time may become limiting (Miquet 1986). The specific foods eaten vary both regionally and in relation to snow cover. When available, Black Grouse prefer to feed on understorey dwarf shrubs, the principal species being either bilberry and rhododendron and female cones and shoots of juniper *Juniperus communis* in the Alps (Zettel 1974, Pauli 1978, Zbinden 1984, Ponce 1985), or heather *Calluna vulgaris* and bilberry in Britain (Picozzi and Hepburn 1984, Cayford 1990, Baines 1994).

Catkins, buds, twigs and needles of a range of tree species are eaten, especially when ground vegetation is covered by snow. Catkins and twigs of birch *Betula* spp. are preferred (Kaasa 1959, Pulliainen 1982, Picozzi and Hepburn 1984, Hjeljord et al. 1995). In the northern taiga, birch may form the bulk of the diet for five months (Seiskari 1962). Buds and catkins of alder *Alnus* spp. and larch *Larix* spp. are also eaten (Pauli 1978, Ponce 1987), as are first year cones and needles of pines, both *Pinus montana* and *P. sylvestris* (Ponce 1985, Pulliainen 1982). During prolonged snow cover in some parts of northern Britain, high mortality has been linked with a lack of suitable foraging trees (L. Waddell pers.comm.).

In northern Scandinavia, established artificial feeding sites attract birds to oats in winter (Marjakangas 1985). Despite the extensive use of feeders by large flocks, numbers of Black Grouse in the proximity of feeding sites in Finland have continued to decline. It would appear that birch trees are preferred to oats and that artificial feeding neither reduces winter mortality (Marjakangas 1987, Willebrand 1988) nor increases reproductive success (Marjakangas and Aspegren 1991). Thus over most of its range, and particularly where preferred tree species are available, Black Grouse may not suffer from a shortage of winter food.

Spring food

Both Brittas (1988) and Willebrand (1988) suggest that breeding success may be correlated with spring levels of body-fat. It follows that the availability of protein and energy-rich food to females in the pre-laying period may be important (Siivonen 1957). At this time, the most commonly eaten plants include the inflorescences of cotton grass *Eriophorum vaginatum* on wet moors (Parr and Watson 1988, Niewold 1990a, Baines 1994) and forest bogs (Angelstam 1983). Overgrazing of these areas by sheep can lead to large reductions in their availability to Black Grouse (Parr and Watson 1988, Hudson 1989). Alternative sources of early spring forage include larch buds and flowers and bilberry stems (Pauli 1978, Ponce 1985, Cayford 1990) and leaves of herbs such as clover *Trifolium* spp., buttercups *Rannunculus repens* and *R. acris* and marsh marigold *Caltha palustris* (A.E. Starling pers. comm.).

Breeding requirements

Several studies have investigated the requirements of broods in a range of different habitats, eg. heathland and moorland (Picozzi and Hepburn 1984, Parr and Watson 1988, Niewold 1990a, Baines 1994), grasslands (Bernard 1981, Magnani

1988) and boreal forests (Borset and Krafft 1973, Kolstad et al. 1985, Brittas et al. 1988). Many of these studies conclude that there are two important components of breeding habitat: tall shrubby or herbaceous vegetation to conceal nests and broods and an abundant supply of invertebrates preferred by young chicks.

The preference of tall vegetation in which to nest is described in Scotland, where nests tended to be located in dense mature heather 50 cm tall with on average 75% overhead cover (Parr and Watson 1988, Picozzi unpubl.). The hypothesis that good concealment is necessary for successful nesting has both supportive (Niewold 1990a) and contradictory evidence (Storaas and Wegge 1987, Brittas and Willebrand 1991).

Most studies agree that chicks prefer to forage in tall vegetation. Bernard (1981) found that the height of vegetation used by broods ranged from 15-70 cm, with a mean height of 35cm. Rushes also provide tall, dense cover for chicks (Parr and Watson 1988, Baines 1994) and in boreal forests, birch and spruce shrubs with 40-60% cover are preferred (Brittas et al. 1988). As well as providing invertebrates, tall cover can also provide protection from predators for both chicks and adults, the latter being vulnerable to predation by raptors (Angelstam 1984, Willebrand 1988).

Invertebrates form the majority of the chick's diet for the first two to three weeks after hatching (Kastdalen and Wegge 1984, Ponce 1992). Broods selectively forage in habitats rich in invertebrates (Picozzi and Hepburn 1984, Baines et al. 1995a), with high chick mortality correlated with low invertebrate abundance (Picozzi and Hepburn 1984, Niewold 1990a). Larvae, both of Lepidoptera and sawflies (Symphyta, Hymenoptera) often together with ants, form most of the diet (Kaasa 1959, Niewold 1990a, Cayford 1990, Ponce 1992, Picozzi unpubl., Starling unpubl.). These items tend to be found in greatest quantity in damp grass or rushy mires amongst heather moorland (Picozzi and Hepburn 1984, Niewold 1990, Baines 1994), in association with bilberry on forest floors, particularly old forest (Kolstad et al. 1985, Baines et al. 1995b), or in alpine meadows (Magnani 1988).

Reductions in the quality of brood habitats result from management practices that cause losses of tall vegetation for nesting and brood rearing and fewer associated invertebrates preferred by chicks. Such practices include overgrazing by domestic livestock or red deer *Cervus elaphus*. Fewer broods and lower breeding success were found on moorlands where grazing pressures were high (Baines et al. 1995a). In grassland habitats, earlier mowing dates and intensification of management have resulted in losses of invertebrates, restrictions of brood movements so that broods use unsuitable habitat and decreased chick survival (Magnani 1988, Niewold 1990a).

The loss of shrubby birch and spruce cover from older stands of boreal forest as a result of mechanical cleaning before the last thinning has also reduced the quality of brood rearing areas (Brittas et al. 1988). In addition, clear cutting of stands of old forest reduced the invertebrate abundance by more than 95% (Stuen and Spidsø 1988).

Spatial ecology

The number, size and possibly isolation of habitat islands contribute most to explaining spatial as well as temporal differences in Black Grouse abundance, both in boreal forests (Angelstam and Martinsson 1990) and in southern and central Europe. Telemetry studies in Britain suggest that the three potentially limiting requirements, a protein and energy rich food source in spring, trees and shrubs in winter and insect rich tall vegetation for chicks, are generally met within a home range of 300-500 ha per lekking group (Picozzi and Hepburn 1984, Cayford 1990). Searches for leks in northern Britain found that in suitable habitat the mean inter-lek distance was about 2 km (Robinson et al. 1993. Assuming spherical, non-overlapping home ranges, this too suggests that each lekking group of males utilizes an area of c.320 ha, but females may travel several kilometres to visit a lek (L. Ellison pers. comm.) and return to breed much further from the lek (T. Spidsø pers. comm.).

In the boreal forest, lekking groups of males were found in habitat patches of mean size 1.6 km^2 (range 0.9-3.4 km^2). Variations in density were strongly correlated with the number and size of preferred raised bog, clear-cut and young forest habitats and explained 84% of the variation in numbers of birds attending leks (Angelstam 1983).

Land use practices that cause the fragmentation of habitats and the consequent isolation of small groups of birds will tend to result in local extinctions, particularly at the edge of a species' range (Fritz 1979, Ellison et al. 1984). These preferred forest patches typically last for up to 20 years (Swenson and Angelstam 1993). Hence, even if the overall population is stable, sub-populations in each patch are highly dynamic and local colonizations and extinctions are frequent and track the dynamics of habitat patches (Angelstam and Martinsson 1990). It follows that patches of good habitat must be protected, even if the species is not yet there. A similar scenario occurs in Britain, where many Black Grouse populations are increasingly restricted to pre-thicket stages of commercial plantation forests (Thom 1986, Grove et al. 1986). Young stands with tree canopy covers of 15-40% can support high densities of Black Grouse, but when canopy cover exceeds 70% after some 12-15 years, few if any birds remain (Cayford 1990, Baines unpubl.).

The extent to which the fragmentation and increasing isolation of patches of suitable habitats affect Black Grouse is not fully understood. The minimum number of birds and the area of habitat needed for the long-term persistence of a population is not known, but will be largely related to the dispersive capacity of juveniles and to habitat quality. Young males tend to be poor dispersers and most recruit into the nearest lek. However, natal dispersal in females averaged 6.3 km in Sweden (Willebrand 1988) and over 10 km in Finland (Marjakangas et al. 1991). Seasonal movements of up to 9 km between summer and winter home ranges by both sexes are frequent in the French Alps (Ellison et al. 1989), and up to 20 km in Finland (Marjakangas et al. 1991). No such long distance seasonal movements have been recorded from Britain. A theoretical minimum viable population of 60 females requiring 2000-6000 ha has been suggested for the French Alps (Ellison et al. 1984), but Niewold (1990b) suggested only 25 females in a core area of 1000 ha, surrounded by sympathetically managed buffer zones in the Netherlands.

Required research

I suggest three major areas of research that need to be conducted.

Habitat research

Habitat fragmentation and dispersive capacities The acceptable degree of isolation of habitat patches needs more accurate determination. More information on colonization and extinction rates from patches varying in size, isolation and quality are needed. The role of dispersal in determining these rates needs to be described, with particular emphasis on how females respond to fragmentation.

Experimental management trials Grazing pressures and forest structures need to be experimentally manipulated to determine optimal conditions for Black Grouse, particularly for brood rearing. Replicated trials involving removal of predators should be considered where increasing numbers of predators, eg. Goshawk *Accipiter gentilis* and red fox *Vulpes vulpes* in Central Europe, threaten populations near to extinction.

Harvesting models and survival rates Black Grouse are still widely shot. Greater awareness of the effects of hunting must stem from a comprehensive knowledge of population dynamics, particularly natural survival rates from a range of sites in relation to precise and compatible kill statistics. Initial work in the Alps, suggests that one result of hunting was low numbers of males, associated with distorted sex ratios (Bocca 1987, Ellison et al. 1988), whilst in Finland harvesting rates in excess of 10% (both sexes shot) resulted in declines of Black Grouse (Linden and Sorvoja 1992). Harvesting models should be built to provide advice to hunters on the number of birds that can be cropped.

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Summary

This paper reviews some of our knowledge on Black Grouse and identifies some gaps that need to be filled by further research. Although Black Grouse occupy a wide range of habitats and eat a broad spectrum of foods, some habitat and dietary features are common to most populations. These include protein-rich food in the pre-laying period, primarily flowers of cotton grass, but also buds of larch and growing tips of herbs, tall vegetation providing cover for nesting and invertebrates for chicks, and trees, particularly birch, during snow conditions in winter. These elements should be represented within habitat patches of not less than 3-400 ha for each lekking group. Fragmentation of habitat patches resulting in localised extinctions is of concern, but the degree of fragmentation that is tolerable is unknown. Future research priorities should assess both this aspect and the impact of predation and continued hunting on already declining populations.

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Habitat requirements of Capercaillie

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Introduction

During the last few decades, Capercaillie *Tetrao urogallus* numbers have been declining throughout its range. In central Europe, many local populations have disappeared. Since the 1970-1980s, hunting has been stopped in Scotland and parts of the Continent, but could not stop the decline. Loss and deterioration of habitats are assumed to be the major causes of decline (e.g. Klaus et al. 1986, Rolstad and Wegge 1989, Storch 1995). Habitat changes occur at various levels of spatial scale. As a habitat specialist, Capercaillie may be sensitive to local changes in habitat structure, i.e. habitat features at forest stand level. Due to its large spatial requirements, however, Capercaillie are also susceptible to forest fragmentation.

Conservationists have been trying to increase numbers of Capercaillie by habitat management. Most such programmes operate locally. Recently, several Capercaillie management recommendations have been drafted on international (European Community), national (e.g. Britain (Crockford and Williams pers. comm.), Switzerland (Marti pers. comm.)), and regional (e.g. Thuringia (Klaus et al. 1985), Black Forest (Schroth 1990), Voges (L. Ellison, pers. comm.)) scales. However, we still lack general guidelines to Capercaillie habitat management.

As a first step towards such guidelines, the participants of the 6th International Symposium on Grouse at Udine asked me to summarise our present knowledge about Capercaillie habitat requirements. As a result, this paper aims to point out the general pattern rather than local peculiarities in Capercaillie habitats. It may serve as a basis for discussion among grouse researchers, and as a guideline for habitat improvement which should be refined by further research and management experiments.

The primary habitat of Capercaillie

The Capercaillie is a northern species, adapted to boreal climax forests. Its main distribution is in the taiga of the north-western Palaearctic. The primary habitat of the Capercaillie is a landscape dominated by old-growth forest intermixed with bogs and patches of younger successional forest stages following natural disturbance such as wind-blow, snow-break, and fire. The forests are characterised by coniferous trees, open structure with moderate canopy cover, and rich ground vegetation dominated by bilberry *Vaccinium myrtillus* and other ericaceous shrubs (see review in Klaus et al. 1986).

Old natural forest - a conditio sine qua non?

In the temperate zone, e.g. in central Europe, where the natural vegetation mostly is deciduous forest, both coniferous forests and Capercaillie are restricted to montane regions (Klaus et al. 1986). Compared to the boreal forest, most central European conifer forests are rather dense by nature. Here, Capercaillie abundance was highest not in the early times of virgin forest, which was dense and dark, but at times when human land use practices created suitable secondary habitats, e.g. during the 18th and 19th Centuries. Then, cattle grazing and collection of forest litter by peasants kept the soils poor and allowed light to reach the forest floor, favouring the growth of pine and bilberry (Klaus et al. 1986). The forest structures resembled the Capercaillie's primary boreal habitat.

These historical records indicate that managed forests are not necessarily disadvantageous to Capercaillie. Appearently, Capercaillie depend on particular habitat structures, but are rather flexible with regard to conifer species and forest age. In most areas, old, natural or semi-natural forests are the Capercaillie's stronghold, because they best meet its structural habitat needs (Rolstad and Wegge 1987, Picozzi et al. 1992, Storch 1993a). However, Capercaillie forests need to be neither "old" nor "natural". There are many examples of young and commercial forests used by Capercaillie. Today, the best Capercaillie populations of the Bavarian Alps are found in managed forests with even-aged, spruce-dominated stands (Storch 1993 b). Both in Scandinavia and in Scotland, Capercaillie were reported frequently to use plantations, even those of introduced conifers such as Sitka spruce *Picea sitchensis* (Rolstad and Wegge 1989, Picozzi et al. 1992). As long as trees with branches strong enough for perching and winter feeding are provided, even young stands may be used by Capercaillie.

Studies throughout the distribution range confirm that Capercaillie select habitats that resemble its primary habitat, the boreal forest. This bears an important implication to Capercaillie conservation: habitats may be improved by creating such structures. The features of the boreal forest may be used as a guideline to Capercaillie habitat management.

In Capercaillie conservation practice, there is some confusion between the habitat requirements of viable populations, and the habitat use by individuals. Individual Capercaillie can be found in a wide variety of habitats. They may use forest stands without a single bilberry shrub, may nest on the bare ground of pole stage stands, and may even visit human settlements. However, the preferences of the species are much narrower than the range of habitats used by individuals. In the following, I try to use these preferences to characterise *good* Capercaillie habitats, i.e. habitats which are likely to sustain viable Capercaillie populations.

Features of good Capercaillie habitats

1.Tree species composition

Capercaillie largely rely on conifers for winter food. There is only one example from the Cantabrian mountains in Spain, where they take holly *Ilex aquifolium* instead of conifer needles. Among conifers, Scots pine *Pinus sylvestris* is the preferred food plant (Jacob 1987). In some areas of Siberia, however, *Pinus cembra sibirica* is preferred over *P. sylvestris* (Klaus et al. 1986). Where pine is absent, Capercaillie prefer fir *Abies alba* over spruce *Picea abies*. In the Bavarian Alps, they eat 95% fir needles in a forest of 80% spruce and less than 10% fir (Storch et al. 1991). In some areas, however, they live in pure spruce forests. Deciduous trees seem not to be vital, although Capercaillie may locally take many beech *Fagus sylvatica* buds in spring (Jacob 1987).

As a guideline, good Capercaillie forest should be dominated by conifers, i.e. at least 70% coniferous trees. The preferred native feeding tree species should occur throughout most of the area and should account for at least 10-20% of the trees in all seral stages.

2.Forest structure

Capercaillie prefer forests with a well-developed field layer that provides food and cover. Vegetation of 30-40 cm in height is tall enough to hide, but not too high to watch out for predators (Klaus et al. 1986, Storch 1993c, 1995). Cover and height of the ground vegetation depend on the light conditions on the forest floor, and thus on canopy cover. Therefore, dense forests are unsuitable as Capercaillie habitats. Furthermore, Capercaillie are large birds, and cannot fly through dense stands. In managed forests both in Scandinavia and in the Alps, Capercaillie were found to prefer stands with canopy cover of about 50% (Gjerde 1991, Storch 1993a, c). In the Bavarian Alps, these are the conditions where the proportions of bilberry shrubs in the ground vegetation are highest (Storch 1994a).

Generally, moderate canopy cover and a good ground vegetation are features of the latest stages of forest succession. In younger forest age classes, however, similar structures may be found where the canopy is opened up, e.g. along forest roads, logging tracks, or at gaps due to wind or snow-break. In dense forests, Capercaillie may prefer such edge habitats (e.g. Jones 1982, Klaus et al. 1985, Klaus et al. 1988, own observations from the Alps), because they create suitable habitat structures. However, it cannot be concluded that edges are an important habitat feature *per se* (Storch 1993a).

"Edge" is a rather dangerous term because it bears a high potential for misunderstanding. To increase the amount of edge may enhance the quality of Capercaillie habitat where edge results from small openings in an otherwise dense forest. However, highly fragmented remnants of old-growth forest are also rich in edge, but doubtlessly unfavourable to the Capercaillie (see below). Therefore, the term edge should better be banned from descriptions of Capercaillie habitat requirements.

To create conditions that lead to a well-developed ground cover should be one of the major aims of Capercaillie habitat management. Where forests are too dense, thinning and the creation of gaps will be helpful. In even-aged forests, canopy cover of about 50% may be used as a guideline. In central Europe, mixed coniferous forests managed by selective cutting tend to have a rather dense, multilayered structure with plenty of natural regeneration. Such forests are often too dense to be good Capercaillie habitats, but may support high numbers of Hazel Grouse *Bonasa bonasia* (own observations). To manage for Capercaillie, the understory of such forests should be thinned. In the past, a similar effect was achieved by collection of forest litter and by cattle grazing (see above).

3. Bilberry

Among ground vegetation types, Capercaillie strongly prefer bilberry (e.g. Klaus et al. 1986, Storch 1995). Bilberry is the preferred food source of adults and older chicks (Jacob 1987, Spidsø and Stuen 1988), and provide good hiding cover. Furthermore, bilberry shrubs hold high insect numbers, which is a vital food of young chicks (Kastdalen and Wegge 1985, Stuen and Spidsø 1988). The unique advantage of bilberry is to provide simultaneously optimal adult and chick food, hiding cover, and thermal cover throughout the snow-free season. These functions can only partly be substituted by other types of ground vegetation (Storch 1995).

The amount of bilberry cannot be too high in Capercaillie habitats. At least in the Alps, bilberry develops best in forests with moderate canopy cover of about 50% (Storch 1995). Thus, the availability of bilberry may be improved by thinning of dense forest stands. Other factors that limit the growth of bilberry, such as browsing by deer and livestock, should be controlled. Foresters should neither use fertilisers, which favour the growth of grasses instead of ericaceous shrubs, nor insecticides (see Storch 1994a).

4. Forest mosaic

Landscape ecological aspects have long been neglected in Capercaillie conservation. Only recently, Norwegian studies showed that fragmentation of old forest may lead to enlarged home ranges and reduced survival in Capercaillie (Rolstad 1989, Gjerde and Wegge 1989, Wegge et al. 1990). The number of cocks at a lek is limited by the area of old forest surrounding the lek; patches smaller than 50 ha rarely contain leks (Rolstad and Wegge 1987, Picozzi et al. 1992, Storch 1993b). In the Alps, Capercaillie were found to prefer old forest stands larger than 20 ha throughout the year (Storch 1993a,c).

Therefore, fragmentation of suitable Capercaillie habitats should be kept at a minimum. Stands of good habitat should be larger than 50 ha. Clearcuts and other openings should be small, i.e. not larger than 1 ha.

Fragmentation of habitat conventionally means a change in the physical structure of the environment. But not only logging may lead to habitat loss and fragmentation. Particularly in central Europe, there is growing concern about the effects of human leisure activities on wildlife.

Heavily frequented ski-slopes and hiking-trails may exclude Capercaillie from otherwise suitable habitat (Meile 1982, Miquet 1986, Menoni et al. 1989). Thus, besides the physical fragmentation of habitats, human disturbance may lead to functional fragmentation of the habitat. This kind of fragmentation should also be kept at a minimum.

5. Landscape characteristics

Capercaillie are big birds with large home ranges. During a year, an individual may use several hundred hectares, a lek population several thousand hectares. Although in spring, 10-20 cocks may jointly use an area not larger than 1 km^2 around their lek, the same cocks may spread out over an area more than 10 times that large in summer (Rolstad and Wegge 1989, Menoni 1991, Storch 1993b). A hen may visit several leks, and may breed at a distance of several km from the lek where she mated (Storch 1993b, Moss 1994). Thus, to preserve the lek may not be enough to maintain a lek population.

Capercaillie population densities vary considerably. In some areas of Russia and in Scotland, some 20 birds can be counted per km^2, whereas the 2-4 birds per km^2 estimated for Teisenberg in the Bavarian Alps is a fairly high density for central Europe (Klaus et al. 1986, Storch 1993b, Moss 1994).

We neither have any reasonable estimates of the size of a minimum viable population (MVP) of Capercaillie, nor of its area requirements. Therefore, allow me some guesswork. Capercaillie numbers may fluctuate strongly from year to year. Thus, to be on the safe side, an isolated viable population should probably have several hundred, say 500, birds. In good habitats, these may live in an area of 25 km^2. Elsewhere, however, a population of 500 Capercaillie may require 250 km^2 or more.

All this means that good habitat must be available over a large area, although it needs not to be continuous. As a guideline, at least 100 km^2 of forest with a high amount of good habitat should be provided for an isolated viable Capercaillie population. In my experience, these large spatial requirements and their implications for conservation is the point that is least appreciated among practitioners of Capercaillie conservation. Many central European Capercaillie populations are small and isolated. Because reproductive success of Capercaillie largely depends on weather (e.g. Höglund 1952, Slagsvold and Grasaas 1979, Moss 1985, Kastdalen and Wegge 1990), small Capercaillie populations are highly vulnerable and may not respond to habitat improvement. Therefore, habitat conservation should be initiated long before a population is seriously threatened with extinction. It is our task as scientists to make these points understood.

Summary

This paper summarises our present knowledge about the major habitat requirements of the Capercaillie *Tetrao urogallus.* as a first step towards general guidelines to conservation. The Capercaillie's primary habitat is the Palaearctic boreal forest. This is a landscape dominated by old-growth, open-structured coniferous forest with a ground vegetation rich in bilberry *Vaccinium myrtillus.* Throughout its distribution range, the Capercaillie is associated with habitats that structurally resemble this primary boreal forest habitat. Suitable habitat structures are not restricted to old natural forest, but may be also be provided in managed forests. Good Capercaillie habitats, i.e. those which most likely can sustain a viable population, should be 1) dominated by conifers and include a fair amount of the preferred native feeding tree, 2) sufficiently open-structured to develop a rich ground vegetation, and to allow big birds such as the Capercaillie to fly through the trees, 3) rich in bilberry, 4) little fragmented, with most stands larger than 50 ha, and 5) available over an area of at least 100 km^2.

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Habitat requirements of Hazel Grouse

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Introduction

At the Sixth International Symposium on Grouse, it was proposed that the symposium volume should contain short summaries of what we know, or think we know, about the habitat requirements of the three Eurasian forest grouse species. I prepared the presentation for Hazel Grouse *Bonasa bonasia* based on the literature and on unpublished results from my research and that of my colleagues because a main reason for this exercise was to summarize the present state of our knowledge, including unpublished results. Another goal of the workshop was to identify gaps in our knowledge where further research may be desirable.

P. Helle and H. Lindén (pers. comm.) were sceptical of the value of simple prescriptions to improve forest grouse habitats. They also stressed the importance of considering the spatial aspects of habitat management, especially as the three species differ greatly in their habitat requirements. I agree wholeheartedly with their doubts. I view the ideas presented here as having two uses: 1) to stimulate research on habitat requirements in high-density and marginal populations of Hazel Grouse, and 2) to provide managers with ideas that can be useful for habitat management in areas where Hazel Grouse are acutely endangered with extinction and management decisions must be made quickly if the species is to survive there.

Hazel Grouse have the narrowest requirements for habitat structure among forest grouse in the Palaearctic boreal forest (Seiskari 1962, Swenson and Angelstam 1993). On the other hand, Hazel Grouse are found in a wide variety of habitats throughout their range. These vary from old-growth coniferous forests, coniferous forests managed by selective cutting, group-cutting, and strip-cutting, early successional stages of clear-cut or burned coniferous forests, old-growth deciduous forests, young successional deciduous forest on riparian floodplains, and young coppiced deciduous stands (Bergmann et al. 1982, Scherzinger 1991, Swenson and Danielsen 1991, Swenson and Angelstam 1993). In addition, the winter food of Hazel Grouse varies greatly throughout its range. Because of all this variation, it is easy to concentrate on the differences among Hazel Grouse populations. In such a case, a manager may consider "his" population to be unique, and that research results from other areas are not applicable in his area.

In this summary, I will concentrate on the similarities among Hazel Grouse habitats and populations. I believe that the similarities outweigh the differences and are sufficient to allow general management recommendations. I have divided the habitat requirements into five categories, although they overlap somewhat: cover, winter food, spring food, forest openings, and landscape aspects.

Cover

It appears that Hazel Grouse are not found in open forests because of high predation risk (Lindén and Wikman 1983, Swenson 1991a). One common denominator among Hazel Grouse habitats is dense cover from the ground to about 2 m in height. How dense this cover should be is difficult to quantify because the species occupies both coniferous and deciduous forests. In coniferous forests, it is the coniferous foliage near the ground that is most important, whereas in deciduous forests high stem density is most important. Managed coniferous boreal and montane forest stands dominated by spruce *Picea abies* and/or fir *Abies alba* are suitable from an age of about 10 years (Swenson and Angelstam 1993, Swenson and Klaus unpubl.). Stands become unsuitable at about 50 years of age, after the second pre-commercial thinning (Swenson and Anglestam 1993, Swenson unpubl.). However, if the stand is thinned and spruce/fir regeneration is allowed to grow up, the stand will again become suitable for Hazel Grouse (Eiberle and Koch 1975, Swenson unpubl.). The same situation is seen in deciduous forests, although the period of suitable habitat is shorter (Asch and Müller 1989). Dense young coppiced stands provide excellent cover, and dense young deciduous vegetation after windfalls, as well as the wind-thrown trees themselves, provide cover in old-growth deciduous forests (Wiesner et al. 1977, Bergmann et al. 1982). Unthinned spruce-dominated montane forests in Central Europe are suitable from c. 15 years and onwards because spruce cover remains in the lower forest levels (Kämpfer-Lauenstein pers. comm.). This is also the case in sparsely planted spruce stands in the boreal forest. From this, it appears to be the lower cover that is important, with cover below 2 m most important to Hazel Grouse. However, cover above this height can he important in winter during arboreal feeding, because Hazel Grouse prefer to feed in the upper two-thirds of deciduous trees, where catkins and buds are more numerous (Swenson 1991a).

Hazel Grouse may compensate for habitats with higher predation risk to some extent by spending more time together as a pair (Swenson 1991a, 1993a) or, in some areas, forming flocks in open habitats in winter (Swenson, Andreev and Drovetskii in press). In these studies, birds in groups used more open feeding sites than birds that were alone, suggesting that lone birds would not venture into these more open areas.

Winter food

When snow covers the ground, the diet of Hazel Grouse is dominated by the catkins and buds of deciduous trees. Although the specific foods vary by region, the most important genera are *Alnus, Betula, Sorbus, Fagus, Corylus* and *Chosenia* (Bergmann et al. 1982, Jacob 1988). Hazel Grouse have winter diets richer in protein in colder climates, which explains some of this variation (Swenson, Bonczar and Borowiec unpubl.).

In Fennoscandia, significant correlations were found between the abundance and distribution of winter food (alder) and the abundance and distribution of Hazel Grouse at four levels of spatial scale (Swenson 1993b). However, it is very important to stress the interrelationship between cover and winter food (Formozov 1934). Escape cover should occur within 15 m of winter food trees (Swenson 1993a, 1993b). In areas with little winter food, Hazel Grouse are highly selective in their use of habitats, but where food is abundant, they are less selective (Swenson, Andreev, and Drovetskii in press). For maximum benefit for Hazel Grouse, spruce-dominated forest should have 1 - 10% deciduous trees (alder and/or birch, Swenson and Angelstam (1993)). In a forest dominated by deciduous trees, a certain proportion of spruce may be essential (Wiesner et al. 1977, Klaus 1995), although this has not yet been quantified.

Spring food

The availability of forbs (herbs), growing on nutrient-rich soils, is especially important to female Hazel Grouse during the pre-laying period, when females gain body mass rapidly. Inflorescenses of cottongrass *Eriophorum* spp. appear to be a secondary spring food in the boreal forest (Swenson 1991a). Weather during the pre-laying period had a greater effect on Hazel Grouse reproductive success than in any other time of the reproductive period in all cases where reproductive success or autumn numbers have been compared with weather (Eiberle and Matter 1984, Klaus 1995, Swenson et al. 1994). This indicates the importance of female condition for reproductive success. Also, in Sweden, the size of female territories in spring varied inversely with density of spring food, but male territory size did not (Swenson 1991a). A preference for rich soils (Swenson unpubl.) is perhaps one reason why the Hazel Grouse has not been as negatively affected by nitrogenous input into their habitats via air pollution as Capercaillie *Tetrao urogallus* or Black Grouse *T. tetrix* (Klaus pers. comm.).

Small openings in the forest

Several authors have reported the importance of openings in the forest canopy for Hazel Grouse (Pynnönen 1954, Bergmann et al. 1982, Klaus 1995). Although very dense spruce thickets provide excellent escape cover and good night roost sites (Eiberle and Koch 1975, Swenson and Olsson 1991), these stands provide little or no food on the forest floor. In the snow-free season, virtually all food for both adults and juveniles is taken from the field layer. The forbs and *Vaccinium* shrubs, which are used as food by adult and sub-adult Hazel Grouse and which provide substrate for the insects used as food by young chicks, need light to grow. My experience suggests that it is dangerous for Hazel Grouse to leave dense forest stands to forage along roadsides and other forest edges. Kills by predators occurred significantly more often there than expected (Swenson unpubl.). Openings within the forest, where food plants grew on the forest floor adjacent to dense cover, appear to be the most secure situation. This suggests that optimal habitats for Hazel Grouse should be heterogeneous forests, with a juxtaposition of dense and open areas. The openings should preferably be small, so that they are within the forest and do not form a forest/non-forest edge. Pynnönen (1954) recommended a size of a few hundred square metres for openings, and Klaus (1995) recommended <0.5 ha. Hazel Grouse rarely frequent ground farther than 15 - 20 m from cover (Swenson unpubl.), so that openings do not need to be larger than 30 - 40 m in diameter. However, this size will vary with the forest height and tree density; the important point is that sufficient light reaches the forest floor to stimulate the growth of food plants. If there is cover, such as windthrown trees, in openings, Hazel Grouse will venture further into them (Kämpfer-Lauenstein, pers. comm.).

Spatial aspects of Hazel Grouse habitat

Studies on the spatial aspects of Hazel Grouse habitat are ongoing and unpublished. A review of the data on natal dispersal of forest grouse in Sweden and Finland showed that Hazel Grouse had significantly shorter dispersal distances than Capercaillie or Black Grouse; median dispersal was only 800 m for Hazel Grouse (Swenson 1991b). Also, Hazel Grouse are very site tenacious (Swenson and Danielsen 1995). Thus, as a poor disperser, the Hazel Grouse should be susceptible to habitat isolation.

Our other results to date strongly support this hypothesis. In an agricultural landscape with forest islands surrounded by agricultural land, there was a threshold at about 100 m from continuous forest beyond which few forest islands of suitable Hazel Grouse habitat were occupied (Swenson and Jansson unpubl.). In an almost purely coniferous and intensively managed forest landscape with few patches of Hazel Grouse habitat, a similar pattern was observed. Here, the threshold was around 2000 m (Åberg, Swenson and Angelstam unpubl.). These observations confirm our suggestion that the Hazel Grouse is susceptible to habitat isolation. Hazel Grouse are apparently especially sensitive to the type of forest fragmentation characteristic of much of Central Europe, i.e. forest patches surrounded by agricultural land. This may be a central factor to consider when designing conservation plans for the species; the spatial arrangements of habitats may be just as important as the structure of the habitats themselves. Effects of habitat isolation over the short distances reported here for Hazel Grouse have not been detected for Capercaillie (Angelstam 1983, Rolstad and Wegge 1987), Black Grouse (Angelstam 1983), Spruce Grouse *Dendragapus canadensis* (Fritz 1979), or Sharp-tailed Grouse *Tympanuchus phasianellus* (Temple 1992).

Researchers have assumed that Hazel Grouse can satisfy all their annual requirements within small areas, generally 2 - 15 ha per pair (review in Bergmann et al. 1982). Studies in Sweden have shown that the average annual home range size is about 40 ha (range 18 - 80 ha), based on counts in forest islands of various sizes and on radiotelemetry (Swenson unpubl.). The range of population densities observed in Sweden is within that observed in Central Europe. Home range size varies with habitat quality (i.e. food abundance, Swenson 1991a, 1993b, unpubl.) and juxtaposition of seasonal habitats (Lieser and Eisfeld 1991, Swenson and Danielsen 1994). As a rule, I recommend that 40 ha per pair be used in the preparation of conservation plans, especially when the quality of habitat and saturation density of Hazel Grouse in the area are not known. When dealing with endangered Hazel Grouse populations, it is better to over-estimate the amount of area they require than to underestimate it.

In summary, a landscape should contain c. 40 ha of habitat per pair and these habitat patches should be separated by a maximum of 2 km of forest or 100 m of open fields. The minimum viable population size for Hazel Grouse has not yet been estimated, to my knowledge. Hence, it is difficult to define how much habitat should be preserved in order to maintain a viable population. But if we assume that the minimum viable population size in a stochastic environment is 2,500 - 5,000 adults (Nunney and Campbell 1993), a preliminary minimum estimate of contiguous habitat necessary is 500 - 1,000 km^2.

The primary habitat of Hazel Grouse

As mentioned in the introduction, Hazel Grouse have very narrow requirements for habitat structure, yet occur in a wide variety of management regimes in managed forests and in old-growth forests. Is there a habitat that can be considered the primary one for Hazel Grouse? I propose that there is, and that it is old-growth forest. Old-growth is defined as forest that is old enough to have established a layered vegetative structure due to secondary forest succession in the gaps created in the forest, primarily due to wind-fall, snow-breaking, or other small-scale factors. These stands have internal disturbance dynamics, which create a diversity of tree ages and vegetative cover over short distances (Hofgaard 1993), so that patches of vegetation with a structure suitable for Hazel Grouse occur commonly and close together in a small-scale mosaic within the stands. I base my conclusion on the following points.

Hazel Grouse are found primarily in wet or moist forests on nutrient-rich soils often near streams and rivers (review in Bergmann et al. 1982). In pristine boreal landscapes, old-growth spruce forests were found in fire refugia in the landscape, especially along streams and rivers. Drier, pine-dominated sites, where fires were frequent (Zackrisson 1977), were not Hazel Grouse habitat.

The type of forest management that has been most favourable for Hazel Grouse is selective, group, or strip cutting that creates a layered forest structure (Teidoff 1951, Tomek 1965, Eiberle and Koch 1975, Wiesner et al. 1977, Swenson and Angelstam 1993). This mimics the internal disturbance dynamics, and therefore the structure, of old-growth forest (Falinski 1986).

Alder, the most important winter food of Hazel Grouse in the western boreal forest, is adapted to wet, nutrient-rich sites and grows in gaps in old-growth forest after windfalls (Falinski 1986).

The Hazel Grouse disperses poorly and, once established, is site-tenacious (Swenson 1991b, Swenson and Danielsen 1995). The is why the Hazel Grouse is susceptible to habitat isolation. Short dispersal distances are expected in species adapted to old-growth forests that are spatially stable and contain suitable habitats within short distances in the stands, but not in species adapted to early successional forest stands, where they must colonize new habitats that appear unpredictably for relatively short time in the landscape.

In the boreal forest, Hazel Grouse population sizes are significantly and negatively related to population sizes of red fox *Vulpes vulpes,* but not to those of pine martens *Martes martes* or Goshawks *Accipiter gentilis* (Small et al. 1993, Lindström et al. 1994, Saari and Swenson unpubl., Swenson unpubl.). In fact, Goshawk populations appear to be more influenced by Hazel Grouse population density than vice-versa (Lindén and Wikman 1983, Tornberg and Sulkava 1990). This suggests that Hazel Grouse are less adapted to fox predation than to marten or Goshawk predation. The red fox is an early succession species in boreal forest (Lindström et al. 1994), but pine marten and Goshawks are more characteristic of older forest (Widén 1989, Storch et al. 1990).

I conclude that for the successful management of Hazel Grouse habitats and populations they must he thought of as a species that is primarily adapted to old-growth habitats, even if the habitat in question is a coppiced wood or a forest managed by clearcutting. The overstorey is less important. Hazel Grouse appear to be adapted primarily to the secondary succession that grows in the gaps of old-growth forest following small-scale internal disturbances. They require both dense vegetation and openings where light reaches the forest floor within the forest, and individual grouse do not require large areas. Old-growth forest on wet areas is spatially stable, with gaps occurring throughout, so that Hazel Grouse did not need to develop the ability to disperse widely. This is especially obvious when one considers that these wet or moist old-growth habitats on nutrient-rich soils usually were found along streams and rivers (and still are in the few pristine landscapes we have left). Hence, the suitable habitats occurred as more-or less continuous ribbons throughout the forest landscape. All this suggests that managers of Hazel Grouse habitat must manage for suitable early successional stages of forest while keeping the perspective that the species is best adapted to old-growth forest.

Required research

I suggest that three major areas of research on Hazel Grouse be given priority in the future.

Internal structural aspects of Hazel Grouse habitat.
We know very well where Hazel Grouse are found in relation to available habitats, but we do not know the relationship between habitat structure and important demographic

parameters, such as survival and reproduction. In short, what are the structural characteristics of source habitats (habitats that produce a net export of Hazel Grouse) compared with sink habitats (habitats that receive a net import of grouse)? These characteristics must be determined in a manner that is easily useful to foresters. We have gathered some data on this question in Sweden (Swenson and Angelstam unpubl.), the Czech Republic (Swenson and Klaus unpubl.), and Poland (Swenson, Angelstam and Wesolowski unpubl.), but little is analysed and much more research is needed. Hopefully, the studies of Lieser and Kämpfer-Laurenstein in Germany will be useful here.

Spatial habitat requirements of Hazel Grouse.
I have summarised the data in this area (usually called landscape ecology) in which I have been involved. More information on colonisation and extinction in habitat patches in relation to their size, isolation, and quality may be essential to save the Hazel Grouse in many parts of its range. Åberg and Angelstam (unpubl.) have started an interesting study examining Hazel Grouse occurrence in a pristine boreal forest in Russia, but the studies I have described in this paper should be repeated in Central Europe.

Population dynamics of Hazel Grouse.
Long-term counts of Hazel Grouse, preferably with measures of reproductive success, are necessary so that we can estimate the minimum viable population size for Hazel Grouse and thereby estimate how much habitat is required. Such counts would also be useful for managing hunting in secure populations. Some long-term counts exist (Gavrin 1969, Semenov-Tyan-Shanskii 1983, Leclerq 1988, Romanov 1990, Klaus 1995, Beshkarev et al. in press, Saari and Swenson unpubl., Swenson unpubl.) and it may be adequate to analyse these data for a first estimate of minimum viable population size. Nevertheless, long-term counts from throughout the species' range are important. A reliable method for counting is available (Swenson 1991c), but its use may be limited where population densities are low because much effort is required for each bird found (Huboux et al. 1994).

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Summary

I review our knowledge of the habitat requirements of Hazel Grouse *Bonasa bonasia.* Although they occupy a wide variety of habitats, several important common features are apparent. I argue that the Hazel Grouse is a specialist that is best adapted to secondary forest succession in gaps created by small-scale disturbances in old-growth forest. Important features of Hazel Grouse habitat include the following.

- dense cover in the understorey, especially up to about 2 m in height. This cover can be either coniferous, or high densities of shrubs or young deciduous tree stems, or even windthrown trees.
- adequate winter food, specific to the region, but usually catkins and/or buds of *Alnus, Betula, Sorbus, Fagus, Chosenia,* or *Corylus*
- spring food, primarily forbs or, in some areas, inflorescenses of *Eriophorum,* for the females in the pre-laying period
- small openings in the forest where adult and young Hazel Grouse can forage on the field layer with little exposure to predators
- Spatial aspects of the habitat, because Hazel Grouse are sensitive to habitat isolation. Few Hazel Grouse are found in island forest habitats surrounded by open land further than 100 m from continuous forest, or when habitat islands, surrounded by forest that is not habitat, are more than 2000 m apart. Hazel Grouse may require as much as 500 - 1000 km^2 of habitat to maintain viable populations over long periods. More research is required not only to determine the structure of habitats where survival and reproduction are high, but also to determine the required spatial aspects of habitat and to document population dynamics in a way that can be used to estimate minimum viable population size.

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Short communications

The Black Grouse in Denmark, 1978-1993

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At the First International Grouse Symposium in Scotland, H.J. Degn (1978, Woodland Grouse Proc. intern. Symp. Grouse 1: 27-31) predicted that the Black Grouse *Tetrao tetrix* population in Denmark would disappear before 1980. However, in 1980 there were still Black Grouse left at three sites. These were Randbøl Heath (760 ha), Kongenshus Heath (1360 ha), neighbouring Hessellund Heath (c. 1300 ha) and the Vind Heaths (700 ha). The last blackcock at Randhøl Heath was found dead in 1992. At a guess, there were 5 - 10 birds left at both Kongenshus Heath and the Vind Heaths in 1993.

Ulborg State Forest District has administered the practical work in connection with Vind Black Grouse Wildlife Reserve since 1942. In 1980, when I took over as the forest supervisor of this district, only 5 blackcocks could be counted on the lekking spots in the Wildlife Reserve. Twenty years earlier, 50 blackcocks could be seen on the same area.

Since the population seemed so close to extinction, we agreed not to carry out any experiments with the birds. Instead all possible ways within reason to improve the situation were to be attempted immediately.

The district has a long-standing tradition for heath care by means of burning, mowing and sheep grazing. This care was intensified and systematized in five-year plans. We tried to solve the biggest of our problems, namely removing the *Populus tremuloides*, in many ways, chiefly by cows, sheep and goats and with herbicides. It turned out that sheep provided the most suitable solution, so now we have about 450 ewes and their progeny on the payroll. All the sheep are fenced in.

At the same time, we established feeding areas where no herbicides were used. Among others, the crops were buckwheat, flax and sunflower, all of which are rich in linoleic acid. To avoid problems with Goshawks *Accipiter gentilis*, we removed the hedges of spruce in the Wildlife Reserve as well as a small forest close to the feeding areas. Finally, we requested permission to catch the Goshawks, gas the foxes *Vulpes vulpes* and kill the crows *Corvus* spp. in the closed season. Permission was granted and we have been doing this since 1982.

In 1983, we bought 70 ha of heathland next to the Wildlife Reserve and also a 150 ha estate, which increased the Wildlife Reserve by 100 ha of agricultural land and some small forests. The agricultural land was used partly to dam a brook to make four wet areas and partly to establish some large new feeding areas. Some of these areas were used for grazing, others for "weeds with crop". Still others were used for crops that were green in winter, e.g. rye and trefoil, where snow could be cleared for the birds.

In the beginning, we were only able to raise funds for one salary per year and this only in connection with the State forest job creation programme. This programme stopped in 1984 and we subsequently depended on applications to the Hunting Foundation, who received an annual income from game licenses. The foundation is administered by the hunting associations in Denmark. The Hunting Foundation has owned the Wildlife Reserve since 1942. In the course of time its interest in the project has increased. It now gives Dkr. 300,000 a year.

To minimize the influence of the Goshawk, we have removed the tallest stands on the estate that was bought in 1983. Furthermore, we have entered into care agreements with farmers who have land adjoining the north side of the sanctuary. These agreements are made possible due to funding from a new law under the Ministry of the Environment. Over a five-year period, Dkr. 720,000 is being used to compensate the farmers. The background for the agreements is as follows.

> The number of Black Grouse in the Vind Black Grouse Wildlife Reserve has been estimated as shown in Fig. 1. From 1980 to 1983, there was an increase from 5 to 15 males. Since then, the number has declined steadily by approximately one per year. The alarming thing is that there are no "peaks" which might indicate one or more successful broods. Young birds are a very rare sight in the terrain and chicks never appear. Our conclusions are that due to the elimination of predators the old grouse die either from illness or old age, and that there is something wrong with the chick production. The problem may be caused by predation on nests, eggs and chicks, thin-shelled eggs, poor fertilization, sick chicks and lack of food for these. Except for predation, the other factors may be a consequence of changed agricultural practices and lack of wet areas. It is not immediately possible for us to find additional wet areas and we are not sure that the time is ripe for further action against predators such as other birds of prey and mammal predators as well as a more effective method for dealing with crows.

The agreements with the farmers aim to solve the problem of the changed agricultural practice. On the areas in question it is prohibited to use insecticides and only in very few cases herbicides are allowed.

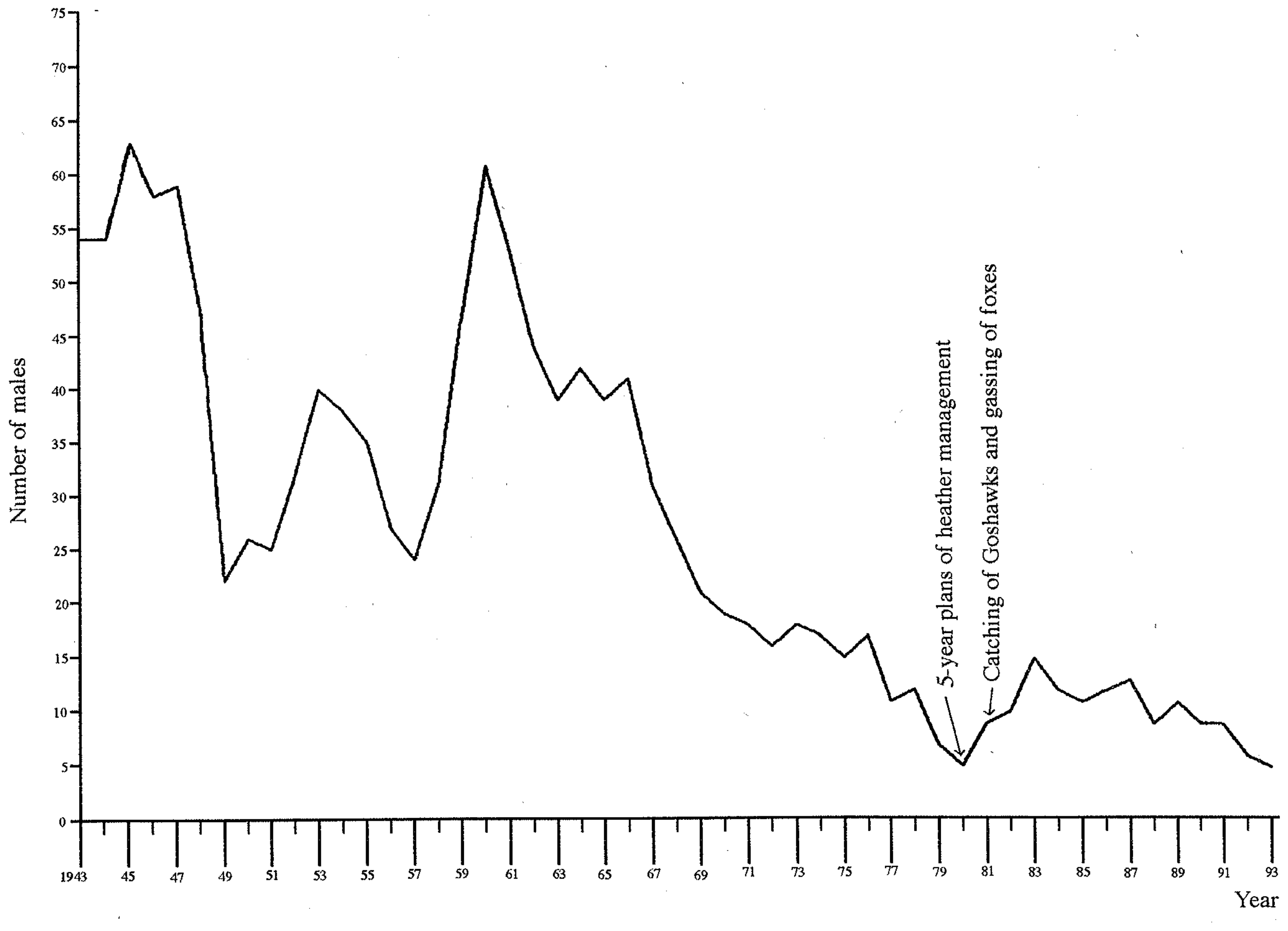
Around the entire heath area we are sowing 20 m broad strips with species intended only for the welfare of the Black Grouse. These areas are not harvested. Fields of stubble are left throughout the winter and the seed corn must not be chemically treated. The background for this last ban is that the Ministry of the Environment has published a survey on the influence of pesticides on birds on arable land. This survey showed that ordinary fungicides, such as Maneb, Thiram, Zineb and Cabtan, induce eggs without shells and increase chick mortality in gallinaceous birds. The fungicides which are used for treating seed corn have not been tested, but since their effect is to kill the fungi, it seems reasonable to assume that birds which live on seed corn for long periods, like the Black Grouse, could have their ability to reproduce damaged.

The Vind Wildlife Reserve and adjoining areas that are suitable for Black Grouse consist of 700 ha of heathland, c. 200 ha of "Black Grouse friendly" agricultural land and c. 100 ha of grazed meadows and willow scrub, in total 1000 ha. In addition to this, 500-600 ha of heathland and meadow areas are situated within a close distance. In 1990, at a Grouse symposium in Holland, Dr Angelstam said that in Sweden there was a capacity of 5 blackcocks per 100 ha (De toekomst van de wilde hoenderachitigen in Nederland, Organisatiecommisssie Nederlandse Wilde Hoenders Amersfoort, 1990, p. 249). From Finnish countings from August 1989, it appears that there is an average density of 12.7 Black Grouse per 100 ha. This means that theoretically there could be 50 to 100 Black Grouse on our areas. This indicates that it is probably not the size of the area that is the limiting factor for our Black Grouse population today.

Another indication that the size of heath is not the only decisive factor is, for example, that Black Grouse are no longer found at Borris Heath (4800 ha, divided between heath, marsh and protected arable land) or Kallesmaersk Heath (2,000 -3,000 ha, divided between heath and protected arable land).

For 13 years now, we have tried almost everything within reason to help the Black Grouse. We hoped that the control of Goshawks and foxes could be a temporary help for some time (see Fig. 1), when we tried to find if the decline in the population could be changed. This could also give the grouse a period to adapt to the present landscape, where the previously extensive heath areas have been replaced by a mosaic of forests, heath, arable land, moor and meadows. If the Black Grouse does not succeed in adapting to this mosaic or if there is some kind of hidden reason for its decline which we cannot find, then its days are numbered.

Fig. 1. Counts of male Black Grouse at Vind Black Grouse Reserve, 1942-93



Morphometric and genetic differentiation of the Black Grouse lineages bred at the Institute for Wildlife Research at Hannover, Germany[1]

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Since 1978, considerable numbers of Black Grouse *Tetrao tetrix* have been bred at the Institute for Wildlife Research (IWF) for research purposes and for scientifically planned release projects.

The founder stock of the stud consisted of four birds of both Bavarian and Dutch origins (i.e. eight altogether), and of 10 birds from Sweden. These three lineages were kept distinct until 1986.

Within the framework of a recently started project, it is hoped that the electrophoretic analysis of numerous genetically determined allozyme and blood plasma protein alleles will shed light on the genetic variability (polymorphism, heterozygosity) within, and the genetic distance between grouse lineages. A correlation between genetic markers and phenotypic traits should provide data on intraspecific differentiation of the species.

The first morphometric data reveal significant differences between Black Grouse lineages of the IWF in body and egg masses, those of birds descending from Swedish stock measuring significantly smaller than those originating from Bavaria or the Netherlands. The differences of the body masses amounted to 97g/133g in males, and to 79g/93g in females. Egg masses: Sweden 31.12g, Bavaria 34.4g, Netherlands 36.41g. Hybrid grouse bred by crossing two of those founder lineages exhibited higher body and egg masses than either of the parental populations.

Genetic analysis of protein variation is a contribution to decide the extent to which the observed inter-lineage variance is due to founder effects, i.e. stochastic sample size effects due to small individual numbers, or to the existence of genetically differentiated regional populations.

Moreover, reintroduction projects would profit from additional data on the following aspects.

1. The regional differentiation of Black Grouse into genetically distinct populations/subspecies.

2. The quantification of genetic polymorphism in relict populations of Black Grouse.

Any colleague willing to support this project with blood or tissue samples from autochthonous Black Grouse populations is requested to contact the authors.

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Status and protection of the Hazel Grouse in China

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This paper discusses the status and protection of two subspecies of Hazel Grouse in China. These are *Bonasa bonasia sibiricus* and *B.b. amurensis*. *B.b. sibiricus* is only found in Yituli River, Kaheigou and Genhe River in Da Xingan Mountain of Inner Mongolia Autonomous Region, and *B.b. amurensis* mainly occurs in Heilongjiang, Jilin and Liaoning Provinces. The Hazel Grouse is a famous game bird and formerly occurred in large numbers in north-east China. Recently, however, because of habitat destruction and hunting, the species is faced with extinction.

Distribution

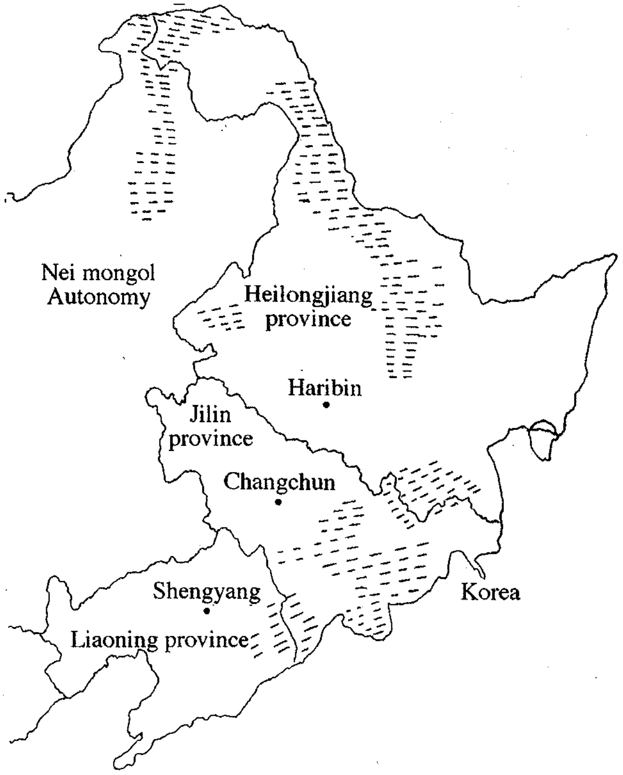
Thirty years ago, Hazel Grouse were one of the more widespread forest birds in north-eastern China and were abundant or common from Da Xingan Mountain, Xiao Xingan Mountain and Changbai Mountain to Dongling of Hebei and Beijing. In recent years, their distribution has diminished remarkably and has become discontinuous. Now, the species has been extirpated from Hebei Province. There are small populations in south-east Liaoning Province including Chao-he-kou, Xinbin, Huanyin, Huadian county, but they are rare in Dongfong, Liube, Hailong, Dunhua county in south-west Jilin Province. They are only abundant in the Changbai Mountain area of east Jilin Province, in Xiao Xingan Mountain area of Heilongjiang and in Da Xingan Mountains areas in Inner Mongolia, Autonomous Region. In the Changbai Mountain area, Hazel Grouse are mainly distributed in Autu, Helong, Jiaohe, Yanji, Fushong, Dunhua, Changbai, Jingyu, Jiang, Hunjiang and Huinan county. In Xiao Xingan Mountain, they are found in Yichun, Wuyun, Jamosi, Mudanjiang, Shonghuajiang and Heihe regions. In Da Xinga Mountain area, they occur in Honghuarqi, Yakesi, Jiagedaqi, Huzhong, Gemhe, Tulihe, and Boketu forest regions

The altitudinal distribution of the Hazel Grouse is also distinct, especially in Changbai Mountain, where it is most abundant from 700 - 1500m. It decreases gradually below 700 m and towards 1500m, and does not occur above 2100m.

Numbers of Hazel Grouse have been dwindling over the last 15 years. In an investigation in 1974 over 187 h from January to December in Toudao to Erado area of Changbai Mountain, 257 individuals were observed. The average number seen on a route count was 1.4 h^{-1}. From August to November, the average was 2.6 h^{-1}. In November, the average sighting was 3.0 h^{-1} (Zhao 1977, Acta Zool. Sinica 20: 4).

In June 1974, we also counted the numbers of responses to the playing of recorded calls in 10 standard plots of 100x 300 m^2 in mixed forests of coniferous/broadleaved species and in pure conifer forests. The results were an average of 0.46 ha^{-1} in mixed forests and 0.13 individuals ha^{-1} in conifer forests.

Figure 1. The distribution of Hazel Grouse in China.



In 1976-78 and in 1982-84, Zhang Xinglu (1985, Jilin Forestry Science and Technology, 4: 26-30) surveyed the same area of Changbai Mountain from August to November. He used the same route count methods. His average sightings per hour were 1.24 in 1976, 1.13 in 1978, 0.50 in 1982, 0.43 in 1983 and 0.40 in 1984. From these counts, the population density may have decreased to about half between 1974 and 1984. In 1989 and 1990 when we surveyed these areas again, no Hazel Grouse was seen. Perhaps this was because the counts took less time in 1989 and 1990. However, in our investigation in 1991, when we walked a 131 km transect over 103 h from April to December, 42 individuals were observed with an average sighting of 0.43 h^{-1}, i.e. slightly more than in 1984. In 1992, 0.45 h^{-1} were seen. Apart from 1989 and 1990, these data (Table 1) suggest a big decrease between 1978 and 1982 and then not much change. In 1983-84, the average numbers of sightings per hour were 0.38 in May - August and 0.55 from November - January (Ma Yeching et al., Heilonjiang Science and Technology 1989: 55-58), slightly higher than at Changbai Mountain at the same time.

The decline in Hazel Grouse population is thought to have been due mainly to excessive hunting and to changes in habitat. Some effective and special management of Hazel Grouse and habitat will be needed in the future. In 1993, the total population in China was estimated to be c. 250,000 birds.

Table 1. Numbers of Hazel Grouse counted in 1974-92 in a study area on Changbai Mountain.

Year	Counting time (h)	Individual birds seen	Nos. of individuals/hr
1974	187	257	1.4
1976	62	77	1.24
1977	96	94	0.98
1978	56	63	1.13
1982	32	16	0.50
1983	58	25	0.43
1984	109	44	0.40
1989	8	0	0
1990	12	0	0
1991	103	44	0.43
1992	22	10	0.45

Ecology

In China, Hazel Grouse mostly inhabit regenerating poplar/birch forest, mixed forests of conifer and broadleaved species, conifer forests and regenerating forests. They nest in April -June in Changbai Mountain and in May - July at Da Xingan Mountain to the north. Perhaps this is related to differences in the climate. Nests have been found under fallen trees or bushes, mostly mere scratches in sheltered places, lined inside with fallen leaves and grass, and made by the female only. One clutch is laid each year, with clutch size 5 - 14, generally 8 - 10 (mean 8.69), based on results from all of China (Table 2).

Table 2. Clutch size of Hazel Grouse based on data from throughout the species range in China.

Clutch size	Number of nests	%
5	2	3.3
6	4	6.6
7	7	11.5
8	18	29.5
9	12	19.7
10	10	16.4
11	4	6.6
12	2	3.3
13	1	1.6
14	1	1.6

During the period of egg-laying, one egg is laid each day. When an egg is lost, another is re-laid to make a full clutch. The incubation is by the female alone. The incubation period is about 21 - 23 days.

Hazel Grouse feed in the forest all year, but feeding sites and food change seasonally. Between winter and spring, they feed mainly in tree crowns. In summer and autumn, they feed in low branches and on the ground, mainly on herbs. Forty-eight species of plants and some insects have been recorded as food (Zhao 1977).

Protective strategies

The decline in Hazel Grouse population in north-east China appears to be mainly due to excessive hunting and poor habitat management caused by heavy clear-cutting and deforestation. Now, the People's Republic of China has developed conservation strategies for wildlife, decreased the amount of deforestation and made one law for protection of wildlife. The Hazel Grouse is included in this law. It is listed "second class" in the list of protection of wildlife. Authorities for nature conservation and wildlife management are conducting a research programme on development and utilization of Hazel Grouse. Some institutes and economic units are also breeding birds in captivity for commercial and protection purposes but have produced a limited number of chicks each year. Mortality has been high and few individuals survive for next year.

Acknowledgements - I thank Pao Zhengji for help in the field investigation, David Jenkins for his editing, and T W I Lovel for financial support to attend the Sixth International Grouse Symposium.

Status of the Hazel Grouse in Hokkaido, Japan in 1923-93

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Introduction

In Hokkaido, the northernmost island of Japan, the Hazel Grouse *Bonasa bonasia* is a popular game bird. However, little is known about its biology because of its secretive habits. This paper discusses long-term population trends, distribution and habitats, based on hunting statistics, questionnaires and field counts in Hokkaido.

Population trend

In Japan, national hunting statistics have been recorded since 1923 (Fig. 1). Annual harvests taken between 1 October and 31 January increased from c. 10,000 birds in 1923 to c. 50,000 birds in 1926-28, and then decreased to 10,000 - 20,000 birds in the early 1930s. In the late 1930s, 30,000 - 50,000 birds were harvested annually. There were no data for 1943-44 because of the Second World War, but a similar fluctuation in bags continued until the 1950s. The annual harvests increased to about 50,000 to 60,000 birds in the late 1960s, and then decreased gradually to c. 5,000 birds in 1991.

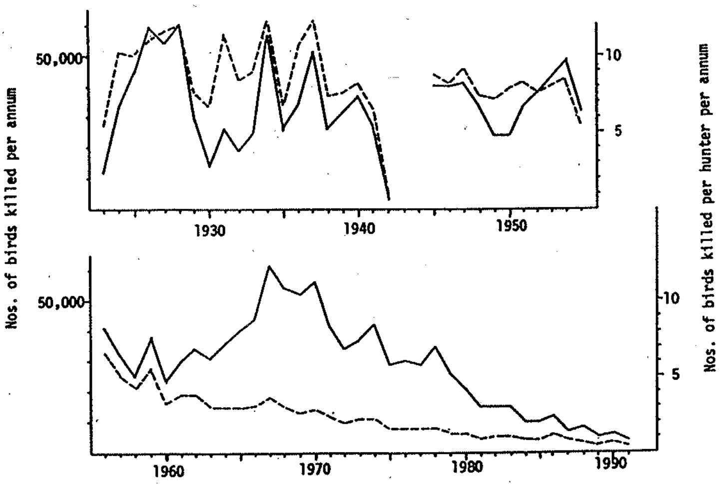

Fig. 1. Numbers of Hazel Grouse killed annually in Hokkaido, Japan, 1923-1991. Solid line - annual harvests; broken line - numbers of birds killed per hunter.

The numbers of birds harvested per hunter changed in a way similar to the total annual harvests until the 1950s, usually c. 5 - 10 birds. Subsequently, the number of birds killed per hunter decreased gradually to 3 in the late 1960s and to 1 in the 1980s and 1990s. These recent decreases coincided with an increase in the numbers of red foxes *Vulpes vulpes* killed both for sport and to control their numbers (Fig. 2).

Distribution

A questionnaire on the distribution and abundance of Hazel Grouse was circulated to 1912 people in Hokkaido in March 1991. The presence of Hazel Grouse was reported from 39% of 3,532 5x5 km quadrats. Hazel Grouse were distributed throughout Hokkaido except for the plains below 1,000 m ASL (mostly residential areas or agricultural lands) and places at high altitude with *Pinus pumila* or alpine meadows (Fig. 3).

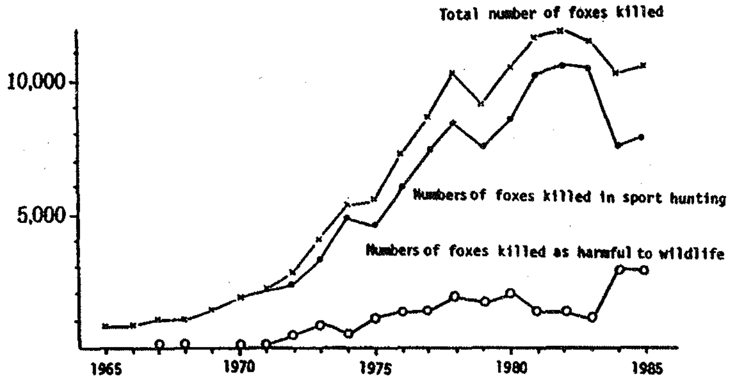

Fig. 2. Numbers of red foxes killed annually in Hokkaido, Japan, 1965-1985.

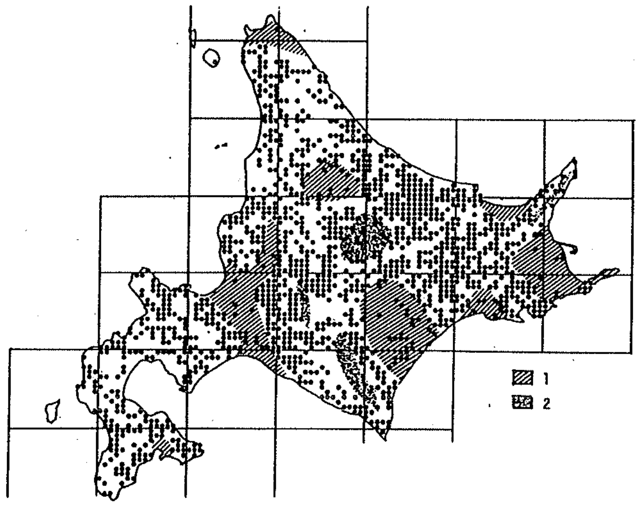

Fig. 3. Distribution of Hazel Grouse in Hokkaido, Japan, based on questionnaires circulated in 1991. Circles indicate quadrats of c. 5x5 km.

key: 1 - plain, 2 - elevation more than 1,000 m ASL.

Table 1. Numbers of quadrats in which Hazel Grouse were observed in various types of vegetation in 1987-93.

Forest type	Total no. of quadrats counted in spring or autumn or both	No. of quadrats in which Hazel Grouse were observed (%)
Coniferous	10	6(60)
Mixed	50	27(54)
Broad-leaved	63	29(46)
Larch plantation	5	0
Pinus pumila	2	1(50)
Others	60	0

Table 2. Numbers of Hazel Grouse counted per 2-km transect in 5x5 km quadrats from late April to early June in 1987-93.

Forest type	Number of birds counted						Mean ± SD
	0	1	2	3	4	5	
Coniferous	6	3	1	0	0	0	0.5±0.7
Mixed	32	21	2	1	0	0	0.5±0.7
Broad-leaved	15	6	2	0	0	0	0.5±0.8
Larch	14	0	0	0	0	0	
Pinus pumila	1	0	0	0	0	0	
Others	60	0	0	0	0	0	

Table 3. Numbers of Hazel Grouse counted per 2-km transect in 5x5 km quadrats from mid-September to late October in 1987-93.

Forest type	Number of birds counted						Mean ± SD
	0	1	2	3	4	5	
Coniferous	4	4	0	0	0	0	0.5±0.5
Mixed	19	13	1	5	9	9	0.7±1.0
Broad-leaved	26	14	6	2	1	1	0.8±1.1
Larch plantation	1	0	0	0	0	0	
Pinus pumila	1	1	0	0	0	0	0.5
Others	2	0	0	0	0	0	

Habitats and abundance

In Hokkaido, forests are mainly classified as evergreen conifer, mixed conifer/deciduous broad-leaved, deciduous broad-leaved natural forests, and larch plantations. In the conifer forests, the main tree species are *Abies sachalinensis*, *Picea jezoensis*, and *P. glehnii*. These occur at middle elevations. Forests below 1,000 m included mixed or deciduous broad-leaved woods dominated by *Acer mono*, *Quercus mongolica*, and *Tilia japonica*, but many other species were present. Evergreen conifer and larch plantations were also found at low altitudes. Dominant undergrowth species were bamboo grass (*Sasa paniculata* in western and central parts, and *S. niponica* in the eastern part). Counts of Hazel Grouse along 2 km line transects in 190, 5 x 5 km quadrats were done in these forests from late April to early June and from mid-September to late October in 1987 - 1993.

Hazel Grouse were recorded in 46-60% of forest quadrats but not in larch plantations. Otherwise, there were no significant differences in frequencies of occurrence of grouse between forests (Table 1). Mean numbers of birds counted per 2 km transect were 0.5 in spring and early summer, and 0.5 - 0.8 in autumn (Tables 2 and 3). There were no apparent differences in mean numbers of birds counted in different types of forests.

Summary

Hazel Grouse were formerly numerous and widely distributed in Hokkaido, Japan, but there has been a big decrease since the 1970s, associated with an increase in red foxes. In 1987-93, sample counts showed Hazel Grouse in 40-60% of natural forests but not in larch plantations. In these natural forests, densities of Hazel Grouse were c. 0.5 - 0.8 birds/2 km transect in sample areas.

Abstracts

Grouse hunting statistics in Russia

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The natural resources of Russia include several species of grouse. The annual bag of amateur and professional hunters in the 1990s included (thousands) Capercaillie *Tetrao urogallus* 700, Black Grouse *Tetrao tetrix* 120, Hazel Grouse *Bonasa bonasia* 2500, Willow Ptarmigan *Lagopus lagopus* 1260, Rock Ptarmigan *Lagopus mutus* 140. The bags of all species of grouse have gradually declined during the last 60 years due both to declining grouse populations and also to some social and economic factors. Captive breeding and re-introduction of some species of grouse could be of great value in conserving wild stocks. The future management and legislation of grouse hunting and the perspectives of co-operative international work in Russia are discussed.

Numbers of grouse and their conservation in Russia

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In Russia, eight species of grouse are recorded as breeding birds. The total number of birds (thousands) according to a count in 1991 was estimated as: Capercaillie *Tetrao urogallus* 1400, Black-billed Capercaillie *Tetrao pavirostris* 670, Black Grouse *Tetrao tetrix* 2975, Caucasian Black Grouse *Tetrao mlokosiewiczi* 60, Hazel Grouse *Bonasa bonasia* 4140, Siberian Spruce Grouse *Dendragapus falcipennis* 1000, Willow Ptarmigan *Lagopus lagopus* 6800, Rock Ptarmigan *Lagopus mutus* 700. Because of the loss of habitats, pollution, overhunting and other reasons, the main trend of populations is more or less towards decline. Caucasian Black Grouse and Siberian Spruce Grouse are already included in the National Red Data Book. Action plans and possibilities for international co-operation are discussed.

Adaptations of the Caucasian Black Grouse to life in the high mountains

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The Caucasian Black Grouse *Lyrurus mlokosiewiczi* is found only in mountains in Caucasus and adjacent parts of Turkey and Iran where it occupies the upper belts of the mountains from the timberline to the snowline, avoiding the forest belt. Its life style is closely connected with steep slopes in the subalpine-alpine zones. Specific features of its morphology and its type of flight and behaviour are adapted to such conditions and show the ancient character of adaptations to the high mountain life. These adaptations include long legs (maximal among tetraonids and like those of the chukar partridges *Alectoris* spp. and snowcocks *Tetraogallus* spp.), the shorter, wider and rounded wing (in comparison with Black Grouse *Tetrao tetrix*), the long and lyre-shape tail of the males and the specific courtship display. The type of flight has a similarity with that of snowcocks; long gliding phases are interspersed with short periods of wing beats. The most prominent behavioural feature is an almost completely soundless lek; males display without any vocalization. The bright black colour of males and their raised (but not fanned) tail makes the birds very noticeable against steep slopes covered by dry yellow grass.

The Caucasian mountains as an ideal region for the introduction of American tetraonids

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The vast area of forests covering slopes of the Caucasian mountains was isolated from the palaearctic forest zones during the whole of the Pleistocene. For this reason there is only one species of grouse in the Caucasian forests. This is the Caucasian Black Grouse *Tetrao mlokosiewiczi* which inhabits mainly the subalpine and lower parts of the alpine zones from the timberline to the alpine meadows. This situation is very favourable for the introduction of some American grouse, for example, Ruffed Grouse *Bonasa umbellus*, Dusky Grouse *Dendragapus obscurus*, and Franklin's Spruce Grouse *Dendragapus canadensis*. The upper parts of the alpine and subalpine zones are free from tetraonids too, and introduction of the White-tailed Ptarmigan *Lagopus leucurus* may be reasonable. The climate and vegetation of the Caucasian mountains are similar to those of the Rocky Mountains so there are no doubts of a successful introduction.

Estimates of Estonian tetraonid populations in 1978-1991 from transect counts

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In each August in 1978 - 1991, transect counts of tetraonids were done in 24 areas in Estonia. The routes over c.500 km were always the same.

Changes in relative density and breeding success of tetraonids were studied. In 1978-1991, minimum to maximum estimates of birds per km^2 were as follows: Capercaillie *Tetrao urogallus* 1.4 - 3.6, Black Grouse *Tetrao tetrix* 3.0 - 4.9, and Hazel Grouse *Bonasa bonasia* 5.2 - 12.1. Relatively poor breeding characterised these populations of tetraonids. Many females seen had no broods. Proportions of young in different areas varied between 17-37%.

Population size and conservation of grouse species in Tian-shan mountain and Altay mountain

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There are five species of grouse in Xinjiang from Tianshan Mountain to Altay Mountain. Capercaillie *Tetrao urogallus* are very rare in Burqin; Black Grouse *Tetrao tetrix* occur mainly over Tianshan Mountain and Altay Mountain with fairly good population status. The Willow Ptarmigan *Lagopus mutus* are extremely rare in Xinjiang. However, the Hazel Grouse *Bonasa bonasia* was common in August and September 1992 on Altay Mountain. Recently, deforestation and tourism have been the main local practices influencing grouse breeding in this environment.

Counting grouse in the Finnish wildlife triangle scheme

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The Finnish wildlife monitoring programme, started in 1988, is based on about 1,500 permanent triangle-shaped routes, each 12 km long. Grouse are counted in February-March and in August. On average, about 7,000 individuals are recorded in late winter and about 15,000 in summer. Late-summer counts are converted to densities (birds are counted only if located within 30 m of the centre-line), whereas winter numbers are only used as indices (all birds irrespective of their distance are recorded). Pooled data from several neighbouring count routes suggest that grouse densities tend to fluctuate synchronously over large geographical areas. Density differences between neighbouring routes may be large, however, due either to small samples or to true small scale variation. Exact locations of observations are recorded, which greatly benefit analyses of spatial and temporal dynamics in grouse populations. Combining site-specific grouse data on forest stands in the same localities with satellite information using GIS based techniques will be a great challenge for researchers in the near future.

The effects of exogenous cadmium on parental behaviour in free-living female Willow Ptarmigan

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Several earlier studies have shown elevated levels of cadmium (Cd) in Willow Ptarmigan *Lagopus lagopus* from areas in southern Norway which are affected by long range atmospheric pollution. In ducks, experimental studies have shown that administration of Cd through the food may alter avoidance behaviour. In this study, we examine the effects of Cd-exposure on parental behaviour in free-living Willow Ptarmigan females. Cd was given as HCdC1 through implants of osmotic pumps. The parental behaviour of Cd-treated females was compared with that of control females. There was no difference in the flushing distance of females with chicks between Cd-treated females and controls. However, Cd-treated females flew significantly further from the brood than control females. Also, Cd-treated females showed less distraction display than control females, although not in all age-categories of broods. The significance of increased exposure of Cd from long range pollution on Willow Ptarmigan is discussed.

Capercaillie display grounds in the Trentino, northern Italy

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In 1990-93, about 90% of (previously known) Capercaillie *Tetrao urogallus* display grounds in the Trentino were monitored and classified, following standard procedures, in relation to the number of displaying males and females and habitat characteristics (exposure, slope, elevation, vegetational features). An estimate of the total spring population size was obtained. This was 1,100-1,150 birds on a potential range of 282,000 ha, with an observed sex ratio close to 1 : 1. Data on forestry management techniques are also discussed, and preliminary results of their application presented.

Capercaillie habitat improvement by adapted forest management

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Clear-cut felling is a very common timber harvest technique throughout the Austrian alps and highland forests. It requires high amounts of silviculture such as cleaning, weeding, thinning and pruning and also high densities of forest roads and cable transportation. However, a few estates manage their forest properties in a more sophisticated and adaptable manner in order to produce more stable stands, more valuable timber of big exploitable sizes, and also more suitable Capercaillie *Tetrao urogallus* habitats. Some long term studies of such practices and of the corresponding very impressive development of local stocks of Capercaillie are demonstrated and discussed. These examples make plain that too large clear-cut areas, and the like, are not only characteristic of an 'inferior' forestry, but also of a less or unsuitable habitat management for Capercaillie.

The impacts of forest die-back on the distribution of Capercaillie leks in north-central Slovenija

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In the course of research on forest die-back in north-central Slovenija, we studied the displacement of leks of Capercaillie *Tetrao urogallus*. By comparing map positions of currently active leks with those formerly used but now abandoned, we found that 44 leks had been abandoned in the East Karavanke Alps since 1945. Most abandoned leks were in conifer forests, predominantly of Norway spruce, on slopes of alpine valleys, within a temperature inversion layer below 1150 m ASL ($n = 33$, $x = 890.5 \pm 152.6$ m, median 900 m). Active leks still occurred at higher altitudes up to 1650 m ($n = 68$, $x = 1244.9 \pm 217.1$ m, median 1300 m). Concentrations of sulphur dioxide in the needles of Norway spruce and the diversity of epiphytic lichens were measured, utilising an index of air purity IAP (Batic 1989). The sulphur content of two-year old needles was tested on 20 sample plots distributed along vertical transects on both slopes of the valley Crna from the bottom (590 m) to the timberline at c.1615 m. The SO_2 content of the needles was found to be inversely related to altitude ($n = 20$, $r = -0.66$). Three different altitudinal zones of forest dieback have been identified: (1) up to 900 m with severely affected trees and large gaps in the canopies, IAP values below 5; (2) 900-1150 m moderately affected, with small gaps in the canopies, IAP values varying between 6 and 13; (3) above 1150 m, less affected, with closed canopies and IAP values 14-22. We suspect that the vertical range of suitable Capercaillie habitats will be further reduced with further emissions of SO_2 in the area.

The effects of patch size and quality on density and reproduction of Black Grouse in boreal forests

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Due to modern forestry practices, the Fennoscandian boreal forest is changing dramatically. The clearcutting technique creates a patchwork of even-aged stands. Depending on ownership, the managed stands vary between10-1000 ha.

The grain concept has been used to describe landscape characteristics. Fine-grained and coarse-grained landscapes are composed of smaller and larger patches, respectively, relative to a given home range size. Almost without exception, a fine-grained mosaic has been assumed to be a superior habitat for wildlife in general, because in a fine-grained mosaic there will be larger amounts of edge leading to higher densities of animals. However, the density of lekking Black Grouse *Tetrao tetrix* males in spring has been shown earlier to be higher in a coarse-grained mosaic.

Numbers of Black Grouse were counted in patches of young forest of different size in August 1990, 1991 and 1992. The density variation was found to be much higher in small patches than in large patches. Neither were there any differences in vegetation quality due to patch size. However, significantly more birds were seen in patches with higher trees, older trees and a higher extent of cover. Area requirement in August seemed to be much lower than in spring.

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