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Patterns and strategies of winter habitat selection in alpine capercaillie

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Based on radio telemetry, habitat distribution of 32 individual capercaillie *Tetrao urogallus* was compared with habitat availability at various levels of scale At forest stand level, capercaillie preferred large patches of late succession stages, and selected for moderate canopy closure and high abundance of feeding trees Hens and cocks selected home ranges with high proportions of old forest, and range size was related to old forest fragmentation Winter survival was high independently of habitat selection In cocks, habitat use was affected by social spacing, home range size and use of old forest were age-dependent, and habitat composition of winter ranges indirectly related to survival and mating success in spring Topography influenced habitat selection, as the birds preferred gentle slopes At the landscape scale, the distribution of bilberry *Vaccinium myrtillus* was the key to capercaillie habitat use, indicating that habitat requirements in autumn and spring influenced selection of winter ranges The study confirms that capercaillie in central Europe select habitats according to structural features typical of the boreal forests of the species' main distribution range However, spatio-temporal variation in resource abundance at the landscape scale sets significant limits to suitability of alpine capercaillie habitats

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Introduction

Due to resource limitation in time and space, winter presents the bottleneck season for many species Grouse, however, evolved in harsh environments, and are well adapted to cope with severe winter conditions Rather than energetic constraints, predator avoidance generally presents the major problem (e g Bergerud and Gratson 1988) Capercaillie *Tetrao urogallus* inhabit boreal and mountainous coniferous forests of the Palearctic. Feeding exclusively on conifer needles (e g review by Jacob 1987, Storch et al 1991), a superabundant forage, enables them to reduce activity in order to minimize energy loss and predation risk (Bergerud and Gratson 1988, Gjerde 1991c) Capercaillie show the most pronounced sexual size dimorphism of all grouse, which is associated with diffential energy requirements and feeding behaviour (Lindén 1984, Rintamaki et al 1984, Storch et al 1991) Hence, intersexual differences in winter habitat selection may be expected (Seiskari 1962) Furthermore, social behaviour may influence spacing patterns and habitat use of individuals (Fretwell and Lucas 1970, Stamps 1991) In capercaillie, males establish display territories within winter ranges (Gjerde and Wegge 1989, Storch 1993), and the spatial organization of the lek may affect winter habitat selection (Gjerde and Wegge 1989)

The objective of this paper is to document patterns of winter habitat selection of alpine capercaillie at hierarchical levels of spatial scale. forest stand (10 ha), individual home range (10^2 ha), and landscape (10^3 ha) My focus is to assess behavioural differences between

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the sexes, and to point out how habitat selection relates to resource distribution, social spacing, and predation risk. The results indicate importance of resource interspersion at forest stand level, and of old forest fragmentation at home range level; at the landscape scale, bilberry *Vaccinium myrtillus* was the key to capercaillie habitat, even in the winter situation.

Study area

The study was done during four winters (December-March), 1988/89 to 1991/92, on Teisenberg (50 km^2), a mountain range in the foothills of the Bavarian Alps, Germany (47°48'N, 12°47'E). Elevations range from 700 m in the valleys to 1300 m in the central part, and 1800 m in the south. Treeline varies between 1300–1500 m in altitude, and only 7% of the area are above 1300 m. Slopes are mostly gentle.

The climate is moist and temperate with mean annual temperatures of 5°C. January is the coldest month with mean temperatures of −3°C, the lowest temperature recorded in the course of the study was −14°C. Annual precipitation averages 1800 mm (1400–2250 mm, 1980–1991). The area is snow-covered from December through April, with snow depth between 0.5 and 2.5 m in midwinter. Conditions for snow-roosting are unfavourable, as the snow surface is mostly firm and crusty. Depending on weather and exposure, snowfree patches may occur throughout winter, and increasingly from late March onwards.

Coniferous forests cover 95% of the area, and are managed by the Bavarian State Forest Service. The remainder are small pastures (2.5%) and alpine vegetation (2.5%) above treeline. Forest stands of varying age form a mosaic with median patch size of 6 ha (range 1–100 ha). Forests have been rejuvenated naturally by opening up strips or patches some 10 yr before felling. Mean rotation period has been 125 yr.

The dominating tree species is Norway spruce *Picea abies* (c. 70%) mixed with beech *Fagus sylvatica* (c. 15%) and fir *Abies alba* (c. 10%). Additional species are rowan *Sorbus aucuparia*, alder *Alnus spp.*, larch *Larix europaea*, and maple *Acer pseudoplatanus*. Bilberry occurs in most of the area and dominates in the central part, while otherwise grass vegetation prevailes. Among potential predators of adult capercaillie, goshawk *Accipiter gentilis*, red fox *Vulpes vulpes*, and pine marten *Martes martes* were common, as judged from the frequency of tracks and sightings. Golden eagles *Aquila chrysaetus*, peregrine falcons *Falco peregrinus*, and beech marten *M. foina* were occasionally observed. There was no predator control, raptors are fully protected in Bavaria, and mammalian predators were only occasionally killed by hunters.

Material and methods

Habitat mapping

Based on forestry maps and aerial photographs (1:10000), I distinguished 558 habitat patches (≥ 1 ha) by successional stage. In the summers of 1989 and 1990, I recorded topography and forest structure within a total of 4500 random plots (radius 10 m, c. 1 plot ha^{-1}). I sampled at least 3 plots per patch, and used mean values of the plots to describe the patches. A habitat map was created based on a geographical information system.

Topographical features measured were altitude (lower slopes 700–1000 m, upper slopes 1000–1300 m, uppermost area >1300 m), exposure, and slope (°). The forest was divided into six habitat types: clearcuts (covered by natural rejuvenation, c. 0–10 yr old), thicket stage (young forest before thinning, c. 10–20 yr), pole stage (after first thinning, c. 20–50 yr), middle aged forest (after second thinning, sparse ground cover, c. 50–90 yr), old forest (final felling stage, well developed ground vegetation, > 90 yr). Uneven-aged stands with small scale (< 1 ha) variation of succession stages were described as "mixed" when no stage comprised ≥ 75% of the area.

Habitat structure was assessed by canopy cover, vegetation layering, tree species composition, tree species diversity, and amount of bilberry in the field layer. Canopy cover, tree species composition (% of total canopy cover), and bilberry cover (% of total ground cover) were estimated to the nearest 10%. The Shannon-Wiener index (Krebs 1989) was used to measure tree species diversity. The number of vegetation layers (1–2 tree layers, shrub layer, field layer) was counted.

Capturing and radio telemetry

I caught capercaillie with mist nets in autumn habitats or in spring at leks. The birds were weighed to the closest 100 g. Hens were aged based on the primary feathers, following Helminen (1963), and all data used here were from adult hens > 1 yr old. Until their 2nd autumn (≤ 15 month), young cocks could be recognized by size and plumage (Klaus et al. 1986), and by weight below 4 kg (N = 3, 3.3, 3.6, 3.7 kg). Fully grown cocks (4.0–4.6 kg, $\bar{x}$ = 4.23 ± 0.19 SD, N = 21) with beak depth ≤ 25.5 mm were classified as two year olds according to Moss et al. (1979) and Wegge and Larsen (1987). Measures from two cocks tagged as yearlings and recaptured as two year olds (23 and 19 months old, 24.5 and 25.5 mm) confirmed this method. Also beyond the second year of life, beak depth increases with age. The beaks of all cocks who were recaptured in later seasons had grown in depth, and a linear regression for cocks of known age (1–5 yr) (i.e. those tagged as ≤ 2 yr olds and recaptured in later years) yielded a significant

Table 1 Size (ha) of capercaillie winter home ranges estimated as convex polygons (range, x̄, SD), by sex and age

Sex	Age	Range	x̄	SD	N
Hens	Adult	10–355	150	122	9
Cocks	Subadult	40–710	284	203	9
	Adult	15–445	128	108	20
	Old	50–225	146	64	6

relation between beak depth and age (calculated in months based on hatching on 1 July), namely (beak depth) = 0 084 (age) + 22 88 ($R = 0\ 86$, $p < 0\ 001$) I distinguished four age classes juveniles (< 1 yr), subadults (> 1 yr, beak ≤ 26 5 mm), adults (beak 27 0–28 5 mm), and olds (beak ≥ 29 0 mm) Subadult age corresponded to the second and third winters, this is the age when cocks get established at leks All adults (c forth and fifth winters) and olds were territorial at the lek in spring, olds were closest to the lek center (see Storch 1993) The only juvenile cock tracked during this study was pooled with the subadult group, as range size and habitat selection were not different

I used 28 g (hens) and 35 g (cocks) necklace transmitters (Kenward 1987) (i e 0 8–1 4% of body weight) with life expectancy of two years The birds were located by triangulation using a portable receiver and a 4-element yagi-antenna Capercaillie are mobile, and their annual (500 ha, Storch 1993) and seasonal (150 ha, this study) home ranges were large compared to mean habitat patch size Thus, to analyse for habitat selection, I considered consecutive daytime locations separated by at least 12 h as independent, and took only one location per bird per night With locations, temperature and intensity (score 0–3) of wind and of precipitation were recorded

Most bearings were taken from forest roads from < 1 km distance Typically 4–6 bearings were taken per fix Based on the size of error polygons, triangulation precision was classified (class 1 error polygon < 0 25 ha, class 2 ≤ 1 ha, class 3 > 1 ha) Accuracy was checked by trials with tags placed 50 cm above ground at locations unknown to the tracker, and when locating incubating females or dead birds Of estimated class 1 locations (N = 30), 80% were within ≤ 50 m from the actual location, 81% of class 2 locations (N = 26) within ≤ 100 m, and 73% of class 3 locations (N = 11) within ≤ 200 m Of all class 1 and 2 locations, 96% were in the right habitat patch For habitat analysis, I omitted class 3 locations, and pooled class 1 and 2 locations a comparison of habitat distribution of class 1 versus class 2 locations did not reveal significant differences (hens $\chi^2 = 6\ 9$, df = 5, p = 0 23, $\chi^2 = 3\ 1$, df = 5, p = 0 68) The data set analysed for habitat selection included 402 hen and 1738 cock locations.

I tracked a total of 32 individuals, 9 hens and 23 cocks I followed 1 hen (82 locations) and 10 cocks (815) in the winter of 1988/89, 3 (70) and 14 (741) in 1989/90, 3 (126) and 13 (349) in 1990/91 and 4 hens (169) in 1991/92 Three hens and 10 cocks were followed for two, and 2 cocks for three winters The data of all years were pooled I estimated 9 female and 35 male home ranges as convex polygons based on 20–107 fixes (x̄ = 53) taken throughout winter

Analyses of habitat selection

Habitat selection was analysed based on comparisons between habitat distribution of capercaillie locations and home ranges, respectively, and habitat availability Most locations (93%) were obtained on the upper slopes between 1000–1300 m Because habitat factors differed between altitude ranges (see below), I estimated availability based on the upper slopes (1000–1300 m) throughout

I assessed selection of successional stages by relating composition of individual home ranges to availability, using Wilcoxon signed-rank matched-pair tests Then, I compared habitat use with availability within each home range Per habitat type I calculated utilization (U) as the frequency of locations and availability (A) as the frequency of this habitat type and calculated Ivlev's electivity index (see Krebs 1989) as $I = (U-A)/(U+A)$ Wilcoxon signed-rank matched-pair tests were used to test observed electivity scores against random utilization ($I = 0$)

To analyse habitat use in relation to time of day (day, 8 am – 5 pm, versus night, 6 pm – 7 am) and weather, I used Bonferroni-Z-tests (Neu et al 1974) To test for effects of weather, I used daytime locations and compared habitat use between locations without (score 0) and with (score ≥ 1) precipitation, low (score ≤ 1) and high (score ≥ 2) winds, and with low (≤ 0°C) and high (≥ 5°C) temperatures

To assess habitat use in relation to forest structure, habitat fragmentation and topography, I compared the distribution of all radio locations with availability I used Bonferroni-Z-tests when availability was known, otherwise, I estimated availability by a set of 2000 random points distributed over the habitat map of the study area, and tested for habitat selection using Mann-Whitney U-tests

Survival

Winter survival rate was calculated following the method of Trent and Rongstad (1974, cit in Krebs 1989), based on daily survival rates. The date of death was exactly known

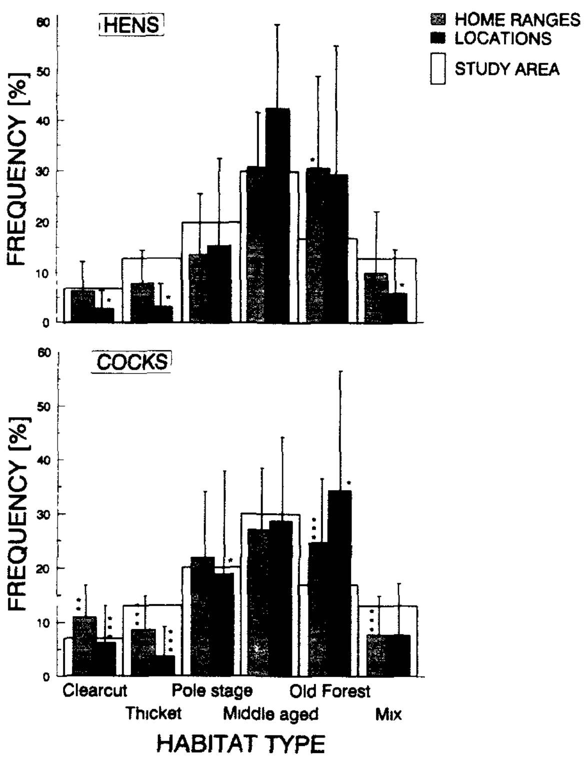

Fig 1 Frequency of habitat types in the study area and in individual home ranges ($\bar{x}$ + SD) of hens (N = 8) and cocks (N = 35), and habitat distribution of locations within home ranges ($\bar{x}$ + SD) Stars indicate significant differences between utilization and availability, stars above grey columns home ranges vs study area, above black columns locations vs home ranges (Wilcoxon-test, * $p < 0\ 05$, ** $p < 0\ 01$, *** $p < 0\ 001$)

Results

Home range selection

Capercaillie used large winter ranges (Table 1) Significant intersexual differences were neither found in range size nor habitat composition For cocks, range size was age-related Subadults had significantly larger ranges than adults and olds ($F = 4\ 38$, $p < 0\ 05$, One-way Anova, Duncan test), and range size of individual cocks (N = 13) decreased with consecutive years ($z = -2.2$, $p < 0.05$, Wilcoxon test)

Capercaillie selected winter home ranges with higher proportions of old forest than available within the area (Fig 1) Home range size as determined by telemetry partly depends on the number of radio locations Estimated range size of hens and cocks was related to the number of fixes they were based on ($r = 0\ 30$ and $r = 0\ 33$, ns) A multiple regression analysis with number of fixes and proportion of old forest within home ranges as independent variables revealed a negative relation between old forest and range size (Fig 2) Due to small sample size in hens, the result was significant only for cocks (hens. $R = 0\ 68$, $F = 2\ 18$, df = 2, 5, $p = 0\ ?$, cocks $R = 0\ 44$, $F = 3\ 74$, df = 2, 32, $p < 0\ 05$) Home range size was not related to middle aged forest, although the birds frequently used this habitat type Also, home range size was independent of availability of the preferred food source, namely fir trees Although old cocks had smaller ranges, no significant age-related differences in home range composition were found

Within their home ranges, hens (N = 8) did not significantly prefer any habitat type, while cocks (N = 34) preferred old forest (Fig 1) However, the use of habitats was age-related old cocks were located in old forest ($\bar{x} = 51\ 3\%$, SD = 21 6, N = 6) more frequently ($t = 2\ 27$, df = 33, $p < 0\ 05$) than adults and subadults ($\bar{x} = 29\ 7\%$, SD = 21 2, N = 29) This was the same in early (Jan–15 Feb) as well as late winter (16 Feb–March)

Effects of daytime and weather conditions

Hens selected habitat types similarly at day and night, while cocks used habitats differently ($\chi^2 = 19\ 6$, df = 5, $p < 0\ 01$) at daytime, they used clearcuts (Bonferroni-Z-test, $Z > 2\ 33$, $p < 0\ 01$) and pole stage ($Z > 3\ 1$, $p < 0\ 001$) more often than at night With low temperatures, both hens ($\chi^2 = 13\ 5$, df = 5, $p < 0\ 05$) and cocks ($\chi^2 = 51\ 3$, df = 5, $p < 0\ 001$) changed their use of habitats Hens reduced the use of pole stage ($Z > 2\ 33$, $p < 0\ 01$), and instead used old forest more often ($Z > 1\ 65$, $p < 0\ 05$) Cocks restricted their use of clearcuts and thickets ($Z > 3\ 1$, $p < 0\ 001$ each), and used middle aged forest more often ($Z > 1\ 65$, $p < 0\ 05$) There were no differences in habitat use due to precipitation or wind, however, strong winds were rare on Teisenberg

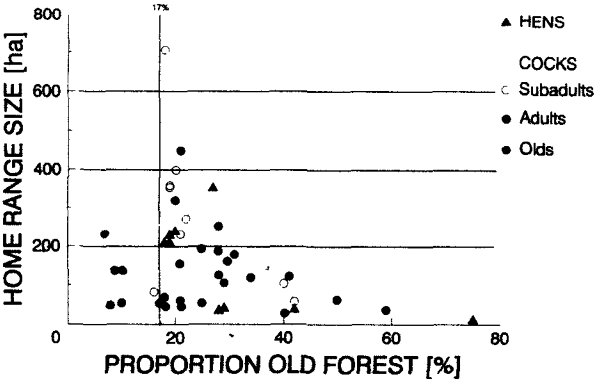

Fig 2 Size of individual winter home ranges in relation to proportion of old forest within the home range, by sex and age class The dashed line indicates availability of old forest on the upper slopes of the study area

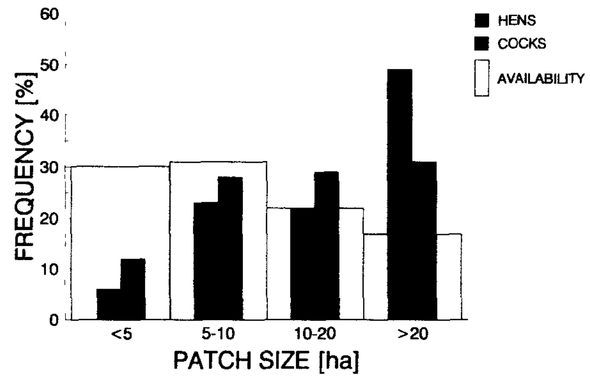

Fig 3 Frequency of capercaillie locations in relation to availability of old forest patches of various size

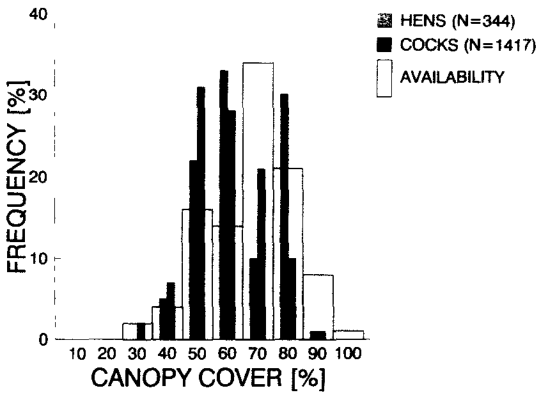

Fig 4 Habitat selection of female and male capercaillie in relation to canopy cover

Habitat structure

When analysing habitat structure, I considered pole stage, middle aged, and old forest Significant intercorrelations between the habitat factors tested were found with tree species composition and diversity (see below), and with canopy cover and layering (r = –0 42, p < 0 001)

Habitat use was affected by forest patch size (Fig 3) Within old and middle aged forest, both sexes were located in larger patches than expected from random distribution (U-tests, p < 0 001 for either sex and habitat)

Hens and cocks selected for low canopy cover (U-tests, p < 0 001 for either sex), but hens used denser forests than cocks (U-test, p < 0 001) (Fig 4) Also within old forest, they selected for less cover (hens x̄ = 50%, cocks x̄ = 51%, p < 0 001 for either sex) than expected (x̄ = 54%)

Regarding tree species composition, both hens (x̄ = 9 9%) and cocks (x̄ = 8 7%) (U-tests, p < 0 001 for either sex) used old forest stands with higher amounts of fir than expected (x̄ = 6 7%) No significant preferences were found concerning any other tree species, nor was a preference for fir-rich stands found with younger successional stages Tree species diversity was inversely related to the amount of spruce (r = –0 6, p < 0 001), and increased with any other tree species, but only hens selected old forest with significantly higher diversity scores (x̄ = 0 53) than expected (0 37) (U-test, p < 0 01) Most forest stands had only one tree layer, and within successional stages, the birds showed no selection in favour of multilayered stands

Bilberry cover in forest stands used by capercaillie was higher (U-tests; p < 0 001 for either sex and habitat) than expected (pole stage. x̄ = 5%; 14%, 8% (expected, hens, cocks); middle aged forest x̄ = 7%, 18%, 23%; old forest 21%, 32%, 55%) Bilberry cover was not related to any other variable of habitat structure

Topographical features

Habitat use of hens and cocks was related to topographical features at landscape level, namely exposure, altitude, and steepness of slope They preferred exposure to NE, E, and SE (Z > 2 33, p < 0 01 each, either sex), and used the other exposures (S, SW, W, NW, N) less than expected (Z > 2 33, p < 0 01 each, either sex) However, east-exposed slopes had higher proportions of bilberry in the field layer than all other exposures, which was significant for NE and E (p<0 001, Oneway-Anova, Duncan test) Exposure was not related significantly to any other of the habitat factors studied

Both sexes were almost never found above 1300 m altitude, avoided the lower slopes (700–1000 m, Z > 3 1, p < 0 001, either sex), and showed a marked preference for the upper slopes (1000–1300 m, Z > 3 1, p < 0 001, either sex) However, habitat factors differed

Table 2 Distribution of some habitat variables in relation to altitude ranges distinguished on Teisenberg (for mean values, x̄ (SD) is given), and proportion of capercaillie locations obtained

Variable	Altitude (m)		
	700–1000	1000–1300	>1300
Area (%)	51	41	7
Slope (°)	16 (6)	19 (7)	36 (11)
Old forest (%)	24	17	1
patch size (ha)	9	6	
Middle aged forest (%)	34	30	11
patch size (ha)	12	13	33
Spruce (%) in total area	62 (26)	81 (25)	29 (30)
in old forest	67 (28)	85 (20)	
Fir (%) in total area	13 (19)	6 (14)	2 (2)
in old forest	20 (26)	7 (11)	
Bilberry (%) in total area	4 (7)	9 (17)	1 (1)
in old forest	6 (7)	21 (25)	
Hen locations (%)	7 5	92 5	
Cock locations (%)	6 7	93 1	0 2

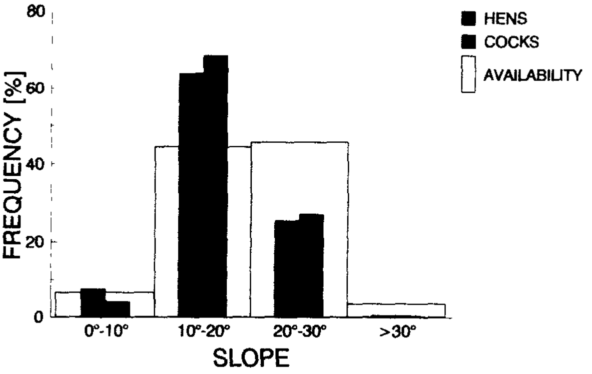

Fig 5 Distribution of locations of female and male capercaillie in relation to slope

with altitude (Table 2) The uppermost areas > 1300 m offered little capercaillie habitat Among the habitat factors preferred by capercaillie, only bilberry cover was better represented on the upper than the lower slopes (U-test, p < 0 001) Within the upper slopes, both hens (U-test, p < 0 01) and cocks (U-test, p < 0 001) used locations less steep than expected (Fig 5) Steepness of slope was not related to any other habitat factor analysed

Survival

Capercaillie were followed for 5713 radio-days during 48 bird-winters One hen (N = 11 winters) was killed by a goshawk, all cocks (N = 37 winters) survived Winter survival rate averaged 98% (sexes pooled)

Discussion

Capercaillie are well adapted to cope with harsh winter conditions Conifers provide thermal cover, concealment against predators, and superabundant forage This continuous supply of resources allows capercaillie to reduce daily activity to 2–3 h (Gjerde and Wegge 1987), and thereby to minimize heat loss and predation risk (Gjerde 1991c) As in most other grouse (Bergerud and Gratson 1988), winter mortality in terms of starvation appears to be negligible for capercaillie, but predator avoidance is a major constraint In Scandinavia, the highest predation of capercaillie was recorded in winter (Wegge et al 1990) Therefore, winter habitat selection should be evaluated in terms of predator avoidance as well as in an energetic context.

Predation risk

On Teisenberg, winter survival was high, although generalist predators were common Due to presumably higher productivity of central European compared to boreal forests, food abundance to predators may be generally higher In addition, food availability may be less reduced by the snow layer Due to micro-topography, snow depth varies on a small scale in the Alps, allowing Teisenberg foxes and martens to feed mainly on small mammals (Storch and Kleine 1991, Ruck 1991) These findings indicate that predator avoidance may be less important in winter habitat selection of alpine than boreal capercaillie

Forest structure and food sources

As described many times from throughout the distribution range (see review in Klaus et al 1986), Teisenberg capercaillie selected open-structured forests of late successional stages In accordance with Scandinavian results (Gjerde 1991a), they preferred canopy cover of 50–60% The literature provides ambiguous views concerning the importance of multilayerd forest structure (e g Glutz von Blotzheim 1973, Eiberle 1976, Klaus et al 1985, Leclercq 1987) On Teisenberg, old forests were used independently of layering throughout the year (Storch 1993, this study). When all seral stages are considered, layering is inversely related to canopy cover, and the selection of open forests might lead to the conclusion that capercaillie prefer multilayered stands According to my results, I conclude that layering per se is no feature capercaillie select for

Despite the low abundance of fir on Teisenberg, fir needles constitute for 90% of the winter diet of capercaillie (Storch et al 1991) As expected, capercaillie preferred areas rich of fir Similarly to the selective use of fir in a forest dominated by spruce, selective feeding on individual trees was described for capercaillie in the boreal forest (Seiskari 1962, Pulliainen 1970, Lindén 1984), as well as for American grouse species (Gurchinoff and Robinson 1972, Doerr et al 1974) Although range size could not be related to the proportion of fir trees, microhabitat selection was probably affected by the position of feeding trees, as was shown for boreal capercaillie (Gjerde 1991b)

Both sexes selected forests rich of bilberry, and bilberry cover was not linked to any other factor of forest structure However, winter ranges of Teisenberg capercaillie are associated with autumn and spring ranges in both sexes (Storch 1993). Bilberry is the staple food during the snowfree seasons The birds take bilberry in autumn until snow-covered, and increasingly in the course of spring. When accessible in winter, bilberry may constitute for ± 10% of the diet of cocks, but never reached > 1% in the diet of hens (Storch et al 1991) As bilberry is no important winter food, foraging preferences at times without snow-cover apparently influenced selection of winter ranges

Adaptations to winter conditions

In the boreal zone, roosting in snow-burrows is an important adaptation of capercaillie to reduce heat loss On Teisenberg, I only observed snow-burrows in early 1988 In the Alps, snow conditions rarely permit snow-roosting My results indicate that alpine capercaillie cope with cold in other terms they minimize movements and stay in feeding trees On cold days, both sexes reduced the use of young successional stages Dense young forest may be advantageous in terms of microclimate, but fir was rare (3%). During cold periods, hens may restrict their activities to local patches of a few conifers for many days (Storch unpubl data), as was described for spruce grouse *Dendragapus canadensis* and blue grouse *Dendragapus obscurus* (King 1971, Herzog 1977, cit in Bergerud and Gratson 1988) Due to smaller size, thermal conduction is higher in females than in cocks, and lower critical temperatures in winter were estimated as +9° in hens, but only −3° in cocks (Rintamaki et al 1984) This may explain why hens led an almost exclusively arboreal life in winter, while cocks frequently went to the ground (Klaus et al 1986, Gjerde 1991a, Storch unpubl data) They may be able to search for scattered ground forage at lower costs than hens, and remained in the trees only with low temperatures

Furthermore, arboreal life may reduce predation risk Hens suffer from higher predation than cocks (Storch 1993), the major predator of hens is the day-active goshawk, while cocks are mostly killed by night-active foxes (Wegge et al 1990) Thus, ground foraging may be less risky for cocks By an arboreal life in winter, capercaillie may minimize both energy loss and predation risk This holds particularly for hens

The role of old forest

Capercaillie on Teisenberg highly preferred old forest, which corresponded best to open forest structure Also, the major food sources, fir and bilberry, were most abundant in old forest Thus, among habitat types, old forest offered the best interspersion of resources Furthermore, on an annual basis, predation risk is lower in old forest than in other habitats on Teisenberg (Storch 1993) As the birds reduced their use of young stages during cold periods, old forest seems advantageous also in an energetic context These results confirm the notion of Rolstad and Wegge (1989), that the important habitat functions are best fulfilled by old forest, although the birds are able to use younger and denser stages

As indicated by the preference for large patches, the use of old forest was affected by habitat fragmentation For cocks, this might result from the location of winter ranges near leks, which were mostly situated in large old forest patches (Storch 1993) However, hens also selected large patches In the boreal forest, predation risk increased with old forest fragmentation (Gjerde and Wegge 1989) I speculate that selection of large patches relates to predator avoidance behaviour, although I could not address this hypothesis in my study

The importance of old forest was confirmed at home range level hens and cocks selected winter ranges with high proportions of old forest, and home range size was inversely related to the amount of old forest Similar findings were reported for boreal capercaillie in spring (Wegge and Rolstad 1986) and winter (Gjerde and Wegge 1989) Compared to figures reported from Norway (Gjerde and Wegge 1989), winter home ranges in the Alps were 5–6 times larger in hens, and 2–3 times in cocks This was not an artifact due to methods of range calculation, a tentative estimate of Teisenberg home ranges with the method used by Gjerde and Wegge (1989) resulted in ranges reduced in size by $<10\%$ compared to the convex polygon method

There are two major differences in resource distribution between Teisenberg and the Norwegian study area Varaldskogen The preferred winter habitat is about twice as common (31% old pine *Pinus sylvestris* forest vs 17% old forest), and the staple food source was almost ten times as abundant (55% pine vs 6% fir) in Varaldskogen (Gjerde and Wegge 1989, I Gjerde pers comm), compared to the upper slopes of Teisenberg This indicates that the large winter ranges observed on Teisenberg are a result of abundance and dispersion of winter habitats and feeding trees

For boreal capercaillie, evidence of intersexual niche segregation due to size dimorphism was reported in the winter situation (Seiskari 1962) On Teisenberg, hens were most often located in middle aged, and cocks in old forest This is in accordance with the notion that hens are less bound to old forest, which is explained by their smaller size and better ability to move in dense cover (Seiskari 1962, Gjerde and Wegge 1989) However, their preference for old forest in range selection, as well as the negative relation between old forest and home range size, show that old forest was key winter habitat for hens as well as cocks

Effects of social behaviour

In cocks, range use was strongly influenced by social spacing Unlike hens, cocks select winter ranges clustered around the lek, and establish display territories within winter ranges (Gjerde and Wegge 1989, Storch 1993) Old forest fragmentation in the surroundings of the lek thus determines habitat composition of winter ranges

Availability of old forest in the winter range of a cock largely determines the proportion of old forest in his display territory of the following spring ($r = 0.72$, $p < 0.001$, Storch 1993), and cocks who survived through the display season had more old forest in their spring ranges than those who died (Storch 1993). Thus, the amount of old forest within winter ranges was indirectly related to individual fitness in terms of spring survival. Therefore, old forest can be viewed as an index of home range quality.

Home range size of cocks was age related. Large ranges of subadults might be ascribed to their tendency for exploratory behaviour (Gjerde and Wegge 1989). However, although winter range quality was not significantly age-related, old cocks stayed closer to the lek center (Storch 1993), and were more often located in old forest. Furthermore, winter ranges of old cocks overlapped less than ranges of subadults and adults (Gjerde et al. 1985, Storch unpubl. data). These findings can be interpreted as the beginning of territorial behaviour. From January onwards, cocks were occasionally heard calling and first aggressive encounters were observed (Storch unpubl. data), indicating mutual avoidance. Later in spring, it can clearly be shown that old cocks occupy the best territories, and force younger competitors to suboptimal habitats in marginal parts of the lek (Wegge and Larsen 1987, Gjerde and Wegge 1989, Storch 1993). Cocks in the lek center perform most of the matings (Hjorth 1970, Muller 1974, Klaus et al. 1986). Hence, there is a gradient in male dominance and reproductive success from the lek center to the outside. Consequently, future reproductive success of a cock relates to the location of his winter range. As preference for old forest may relate to individual fitness in terms of survival and reproductive success, the spacing pattern of capercaillie cocks at the lek fits the model of an ideal despotic distribution (sensu Fretwell and Lucas 1970, Fretwell 1972) (Storch 1993). My results indicate that this pattern becomes established in the course of winter.

Habitat selection at landscape level

At the landscape scale, the habitat features preferred by capercaillie were distributed non-randomly. Independently of topography, old forest was available throughout Teisenberg, except for the uppermost area. However, proportion and patch size of old forest were better on the lower than on the upper slopes, also the amount of fir was higher. Only bilberry cover may explain the pronounced preference of capercaillie for the upper slopes of Teisenberg. This appears striking, as bilberry is snow-covered most of the winter.

In terms of resource availability, the lower slopes seemed to offer the best winter habitats. This might allow smaller home ranges than on the upper slopes. However, the lower slopes bear two disadvantages: first, in vicinity to farmland, predator density may be higher, and secondly, seasonal movements would be necessary between winter ranges and bilberry areas. To stay on the upper slopes allows the birds to remain in the same general ranges from autumn to spring. Due to social organisation of leks, this may be particularly important for cocks, but possibly also for nest site selection of hens. The price the birds pay for staying on the upper slopes in winter is enlarged home range size. In Scandinavia, large home ranges in fragmented habitats were related to high mortality (Gjerde and Wegge 1989). However, as winter survival was high on Teisenberg, increased predation risk is probably a minor consequence of winter habitat fragmentation in the Alps.

There are numerous reports stating the capercaillies' preference for elevated terrain in mountainous forests (see review in Klaus et al. 1986). In most central European distribution ranges, capercaillie disappeared from low altitudes during the last centuries. This probably resulted from changes in forestry: the easily accessible lower forests had been transformed into dense plantations (e.g. von Bulow 1962, Schroder et al. 1982, Klaus et al. 1986). From my results from Teisenberg, I expect that altitude-related differences in resource abundance and possibly predation risk may explain capercaillie distribution at landscape level also in other areas.

Avoidance of steep terrain was repeatedly described for alpine capercaillie (Eiberle 1976, Zeimentz 1981). My results confirm this view, as the birds preferred gentle slopes independently of habitat structure. However, as Teisenberg slopes were gentle compared to e.g. the central Alps, my study could not reveal which degree of slope is critical for capercaillie habitat. Capercaillie were described to select habitats independently of exposure (Eiberle 1976). On Teisenberg, they were mostly located on eastern slopes, which coincided with high availability of bilberry. Therefore, I consider the predominance of eastern exposures in capercaillie locations an artifact due to bilberry distribution.

To summarize, large stands of old forest was the key winter habitat for hens and cocks. My results support the notion that central European capercaillie select habitats according to structural features typical of their main distribution range, the boreal forest: moderate canopy closure, high availability of feeding trees, and luxuriant bilberry cover. Habitat preferences in other seasons influenced the selection of winter ranges. Therefore, habitat use at landscape level was primarily explained by the distribution of bilberry, not only in the snowfree seasons (Storch 1993), but also in winter. This demonstrates that capercaillie habitat selection and spacing patterns have to be seen in an annual context. Capercaillie habitat conservation efforts in central Europe should not remain restricted to habitat structure at forest stand level, but ought to consider spatio-temporal variation in resource distribution at the landscape scale.

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