Oecologia (1993) 95:257–265

Oecologia

Habitat selection by capercaillie in summer and autumn: Is bilberry important?

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Received: 27 January 1993 / Accepted: 10 May 1993

Abstract. The use of habitat by female and male adult capercaillie *Tetrao urogallus* during summer and autumn was studied by comparing the distribution of radio locations of birds with the availability of habitat at forest stand, home range and landscape level in an area of the Bavarian Alps, Germany. Capercaillie preferred forests with structural features typical of their main distribution range, the boreal forest: they selected large patches of old forest with moderate canopy cover of about 50%, and a well developed field layer with high proportions of bilberry *Vaccinium myrtillus*. Hens selected both home ranges and sites within home ranges in old forest. Ranges selected by cocks did not differ from availability in the study area, but they preferred old forest within their ranges. The size of home ranges was negatively related to bilberry cover both in hens and cocks. The distribution of bilberry also determined habitat use by capercaillie at the landscape scale. The study demonstrated that bilberry is the major determinant of the selection of habitat by capercaillie in landscapes with sparse and fragmentary cover of ericaceous shrubs, such as central Europe.

Key words: *Tetrao* – *Vaccinium* – Habitat fragmentation – Habitat selection – Alps

In Central Europe, the capercaillie *Tetrao urogallus* is a highly valued but endangered bird and is considered a key species in conservation of montane forest ecosystems (e.g. Storch and Schröder 1990). Capercaillie are often described as restricted to habitats with structures resembling the forests of the species' main distribution range, the Palaearctic boreal zone. Thus, they are associated with coniferous forest with luxuriant cover of ericaceous shrubs, especially bilberry *Vaccinium myrtillus*. Bilberry is common in most capercaillie habitats (Klaus et al. 1986), provides the staple food during summer and autumn (Jacob 1987), and the eastern borders of distribution of both species coincide well (Klaus et al. 1986). Although the association with bilberry is generally recognized, habitat selection by capercaillie individuals and populations has not been studied in areas where bilberry cover varies strongly on a local and regional scale, such as in central Europe.

During the least few decades, capercaillie numbers have been declining over most of its range. In central Europe, many local populations have disappeared. In the boreal zone, the negative population trend is related to increasing fragmentation of old-growth forests due to forest management (Rolstad and Wegge 1987). Compared to the boreal forest, most central European coniferous forests are productive and rather dense. In the past, capercaillie abundance was highest not in the early periods when virgin forest, which was dense and dark, was prevalent, but at times when land use by humans created suitable secondary habitats, e.g. during the eighteenth and nineteenth centuries. At that time collection of forest litter and cattle grazing kept the soils poor and the forests light, and favoured the growth of bilberry (see review in Klaus et al. 1986). Among the major reasons proposed for the decline of capercaillie in central Europe are vegetation changes due to eutrophication of forest soils, particularly by nitrogen deposition from air and rain (Porkert 1982; Ellenberg 1983; Klaus et al. 1985; Ellenberg 1992). Ericaceous shrubs are increasingly replaced by grass-dominated vegetation (Aerts and Berendse 1988; Högbom and Högberg 1991), a process which may lower habitat suitability for capercaillie (Klaus et al. 1985).

This paper aims to demonstrate the vital role of bilberry in habitat selection by capercaillie during the snow-free season at different spatial scales, from local habitat patches to the landscape level. I describe habitat use of adult capercaillie, as revealed by radio telemetry, in relation to topography, successional stage, habitat structure and fragmentation. Habitat relationships of broods will be dealt with elsewhere.

Material and methods

Study area

Field work was done between June and November 1988 to 1991 in the Teisenberg are (50 km²), a mountain range of the northern foothills of the Alps, Germany (47° 48′N, 12° 47′E). Elevations reach 1300 m in the central part of the area, and 1800 m in the south. The valley bottoms at 700 m altitude are used for dairy farming. The treeline varies between 1300–1500 m altitude. The uppermost slopes above 1300 m offer little capercaillie habitat. The climate is moist and temperate with mean annual temperatures of 5° C and precipitation of 1800 mm.

The area is covered by forests of Norway spruce *Picea abies* mixed with beech *Fagus sylvatica* and fir *Abies alba*. As a result of forestry practices, stands of varying ages form a forest mosaic with patches of 1–100 ha (median 6 ha). Bilberry occurs in most of the area, but at varying densities. It dominates the understory in the central, mostly east-exposed part. Landscape mosaic and forest fragmentation patterns are representative for major parts of the Bavarian Alps. For details of the study area and patterns of habitat fragmentation see Storch (1993a).

Methods

Forest stands on Teisenberg were mostly even-aged. I distinguished 558 habitat patches (≥ 1 ha) from forestry maps and aerial photographs (1:10000), and classified them according to successional stage: clearcuts (cleared areas covered by natural regeneration), thickets (young forest before thinning), pole stage (young forest after first thinning), middle-aged forest (after second thinning, sparse ground vegetation), and old forest (final felling stage, well developed ground cover). Uneven-aged stands with small scale (< 1 ha) variation of successional stages were described as "mixed" when no stage covered more than 75% of the area.

In the summers of 1989 and 1990, I recorded topography and habitat structure within a total of 4500 random plots of 10 m radius; i.e. approximately one random plot per hectare. I sampled at least three plots per habitat patch, and used mean values of the plots to describe the patches (Table 1). I created a digital habitat map based on a geographical information system.

I measured habitat fragmentation by patch size and frequency of edge. Edge included borders of stands of distinct age, forest roads, trails, and gaps within the stand. As measures of habitat structure, I used canopy cover and ground cover, vegetation layering, and composition and diversity of tree layer and field layer. I estimated cover and species composition to the nearest 10%, calculated diversity by the Shannon-Wiener index (Krebs 1989), counted the number of distinct vegetation layers (1–2 tree layers, shrub layer, field layer), and noted the presence of anthills (Table 1).

I caught capercaillie hens and cocks using mist nets in autumn habitats and in spring at leks. I distinguished between juvenile (< 1 year) and adult hens by features of the primary feathers (Helminen 1963), and between juvenile (< 1 year), subadult, adult, and old cocks by beak depth (Storch 1993b). I radio-tagged the birds using necklace transmitters weighing 28 g for hens and 35 g for cocks. When radio-tracking, I recorded temperature and intensity (score 0–3) of wind and of precipitation. Details on methods and analysis of radio-tracking are given elsewhere (Storch 1993b).

I analysed the data separately for hens and cocks, and for summer (June-August) and autumn (September-November). The data set comprised a total of 5262 locations for 38 individuals (Table 2). I followed 5 hens and 12 cocks for two, 3 cocks for three, and 2 cocks for four successive years. Data were pooled for all years.

Table 1. Habitat variables measured in each forest patch

Variable	Measure
Topography	
Altitude	700–1000 m, 1000–1300 m, > 1300 m
Slope	Steepness (°)
Exposure	N, NE, E, SE, SW, W, NW
Forest stand	
Patch size	(ha), minimum 1 ha
Edge	(m/ha), extrapolated from aerial photographs (1:10,000)
Succession	Clearcut, thicket, pole stage, middle aged forest, old forest
Layering	Mean number (1–4) of vegetation layers
Anthills	Proportion (0–1) of plots with anthills
Tree layer	
Canopy cover	Mean (%)
Spruce	Mean proportion of total cover (%)
Fir	Mean proportion of total cover (%)
Beech	Mean proportion of total cover (%)
Larch	Mean proportion of total cover (%)
Other species	Mean proportion of total cover (%)
Diversity index	Shannon-Wiener, based on above groups
Field layer	
Ground cover	Mean (%)
Height	Mean (cm)
Moss	*Bryophyta;* mean proportion of total cover (%)
Fern	*Pteridophyta;* mean proportion of total cover (%)
Grass	*Poaceae, Juncaceae, Cyperales;* mean proportion of total cover (%)
Bilberry	Mean proportion of total cover (%)
Raspberry	*Rubus* spp.; mean proportion of total cover (%)
Regeneration	Trees < 1 in height; mean proportion of total cover (%)
Other species	herbaceous, other than above; mean proportion of total cover (%)
Diversity index	Shannon-Wiener, based on above groups

Table 2. Number of individuals tracked (*n*), and number of locations used for analysis of habitat selection/home range selection

	Summer				Autumn			
	Hens		Cocks		Hens		Cocks	
	n	locations	*n*	locations	*n*	locations	*n*	locations
1988	1	134/134	9	503/568	4	236/261	11	684/742
1989	4	149/299	15	718/833	5	116/127	16	470/529
1990	3	105/132	10	270/293	4	141/142	14	390/397
1991	6	161/297	9	241/253	5	208/214	8	41/41
Total	12	549/862	21	1732/1947	13	701/744	24	1585/1709

For analysis of habitat use, I excluded locations with error polygons >1 ha, and the periods of incubation and chick-rearing of hens (Table 2).

I analysed selection of habitats in relation to topography, habitat fragmentation, and forest structure by comparing distribution of bird locations with habitat availability in the study area. I used the Bonferroni-*Z* approach (Neu et al. 1974) when availability was known. Otherwise, I estimated availability by a set of 2000 random points distributed over the habitat map, and tested for habitat selection using Mann-Whitney *U*-tests.

I used different approaches to evaluate selection of successional stages. First, I compared the distribution of capercaillie locations from summer and autumn, respectively, with composition of the study area, and also tested for effects of time of day and weather conditions on habitat use (Bonferroni-*Z* tests).

Secondly, I related composition of individual home ranges to availability in the study area (Wilcoxon signed-rank matched pair test). As autumn movements of cocks varied in timing between August and December (Rolstad 1989; Storch 1993a), it made little sense to define distinct autumn home ranges. I estimated summer home ranges as convex polygons based on 17–98 ($\bar{x}=45$) fixes taken. Home range size was not related significantly to the number of fixes (hens: $r=0.3$; cocks: $r=0.1$). As range size of hens with chicks was not different from that of hens which lost their clutch, I based female home range estimates on all summer locations, including the periods spent with chicks, when calculating habitat availability within ranges (Table 2).

Lastly, I compared habitat use with availability within individual home ranges. For each habitat type I calculated utilization (*U*) as the frequency of radio-locations and availability (*A*) as the frequency of this habitat type and calculated Ivlev's electivity index (Krebs 1989) as $I = (U-A)/(U+A)$, and tested the observed electivity scores against random utilization ($I=0$; Wilcoxon signed-rank matched pair test).

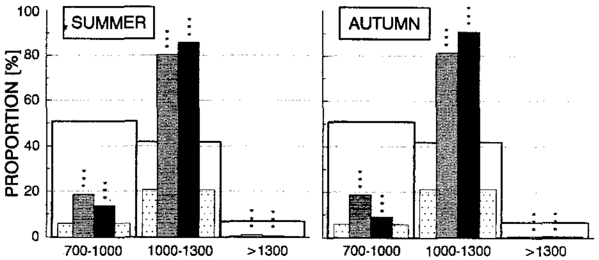

Fig. 1. Distribution of hen *(grey)* and cock *(black)* locations, and mean amount of bilberry in the field layer of old forest *(dotted columns)*, in relation to availability of elevations (% of total area; *open columns*). *Asterisks* indicate significant differences between utilization and availability of elevation (* $P<0.05$, ** $P<0.01$, *** $P<0.001$)

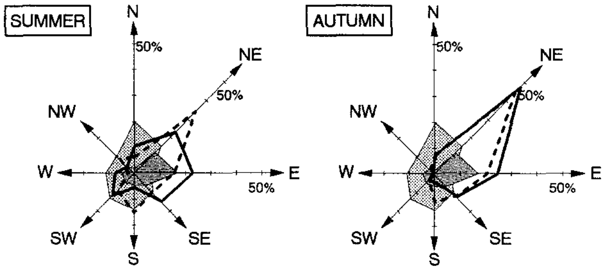

Fig. 2. Distribution of hen *(broken line)* and cock *(solid line)* locations, and mean proportion of bilberry in the field layer *(dark grey)*, in relation to availability of exposures (% of total area; *light grey*)

Results

Habitat selection at the landscape scale

Throughout summer and autumn, hens and cocks preferred the upper slopes at 1000–1300 m altitude (Fig. 1), and mostly selected eastern exposures (Fig. 2). However, both altitude (*U*-test, $P<0.001$) and exposure (ANOVA, $P<0.001$) were related to bilberry cover (Figs. 1 and 2), and not to any other habitat factor preferred by capercaillie. Within this preferred altitude range, they used slopes randomly in summer, and selected slopes less steep than expected in autumn (*U*-tests, hens: $P<0.001$; cocks: $P<0.05$). Steepness of slope was not related to any other habitat factor.

Habitat distribution of capercaillie differed from availability in summer and autumn (hens: $\chi^2=224$ and $\chi^2=293$; cocks: $\chi^2=207$ and $\chi^2=660$; $df=5$, $P<0.001$ for all tests) (Fig. 3). Hens preferred old forest and clearcuts. Cocks also preferred old forest, but unlike hens, they increased their use of old forest from summer to autumn ($\chi^2=253$, $df=1$, $P<0.001$). Habitat use did not differ between daytime (7 a.m.–8 p.m.) and night (9 p.m.–6 a.m.), nor between days with low (score$\leq$1) and high (score$\geq$2) winds, with (score$\geq$1) and without rainfall, or with low ($\leq$10° C) and high ($\geq$20° C) temperatures.

I analysed habitat use in relation to patch size and edge for the upper slopes only (Table 3), because patch size differed between lower and upper slopes, where >80% of all locations were obtained. Within the preferred old-forest habitat, hens and cocks selected large patches. The data revealed a general tendency for selection of large patches of late successional stages, and small patches of young stages. Amount of edge was negatively

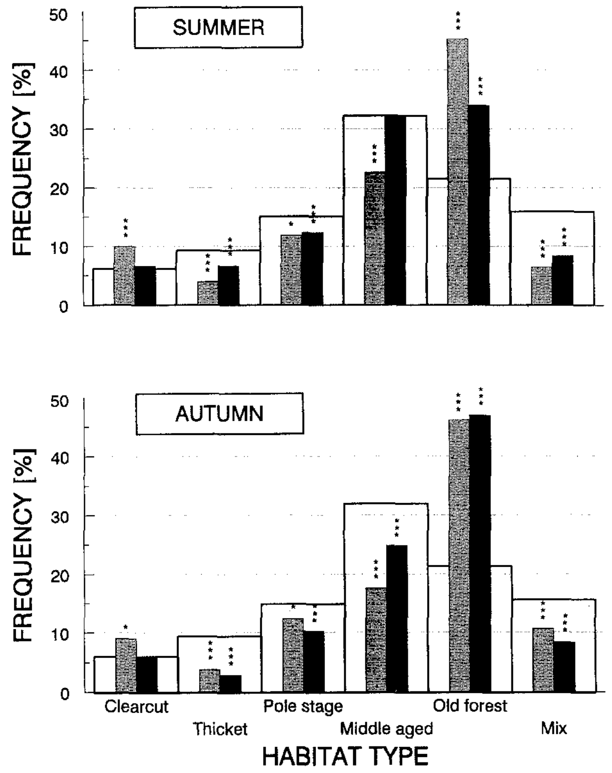

Fig. 3. Habitat distribution of hen *(grey)* and cock *(black)* locations in relation to habitat availability *(open columns)*. *Asterisks* indicate significant differences between utilization and availability (Bonferroni Z test, * $P<0.05$, ** $P<0.01$, *** $P<0.001$)

related to patch size ($r=-0.54$, $P<0.001$ for old forest); when small stands (< median) were excluded, capercaillie showed no consistent selection in relation to edge.

Habitat structure

I analysed distribution of capercaillie in relation to canopy cover and tree species composition in pole stage, middle-aged, and old forests (Table 4). In summer and autumn, the birds selected sites with low canopy cover (U-tests, $P<0.001$ for both sexes and seasons) (Fig. 4). This was not merely due to selection of old forest, als also within old forest, they used stands with lower coverage than expected (U-tests, $P<0.001$ for both sexes and seasons).

In summer, hens showed no consistent preferences in relation to tree species composition. Although the frequency of spruce exceeded 70% in all habitat types, hens selected forests with more spruce and less beech than expected in autumn, as did cocks throughout summer and autumn. The preference for spruce-rich forests may be explained by the positive relation between ground cover and the proportion of spruce (old forest: $r=0.24$, $P<0.01$). As tree species diversity in old forests was negatively related to the proportion of spruce ($r=-0.80$, $P<0.001$), the analysis revealed that capercaillie selected stands with low diversity scores (Table 4). Similarly, the number of vegetation layers was related to spruce cover

Table 3. Median patch size (ha) of various habitat types on Teisenberg, and at capercaillie locations, by sex and season

Habitat type	Teisenberg	Locations: hens				Locations: cocks			
		Summer		Autumn		Summer		Autumn	
	Median	Median	U-test	Median	U-test	Median	U-test	Median	U-test
Clearcut	5.4	5.6	n.s.	5.6	n.s.	5.2	0.05	5.4	n.s.
Thicket	7.3	3.6	0.01	6.0	n.s.	5.7	0.001	5.7	0.01
Pole stage	11.6	13.7	n.s.	12.2	n.s.	12.2	n.s.	12.2	n.s.
Middle-aged forest	19.2	23.6	n.s.	23.6	n.s.	23.6	0.001	32.8	0.001
Old forest	8.6	21.1	0.001	21.5	0.01	13.2	0.001	13.2	0.001

Differences from random utilization are indicated by the results (P value) of U-tests

Table 4. Habitat selection by capercaillie within old forest, by sex and season

Variable	Teisenberg	Locations hens				Locations cocks			
		Summer		Autumn		Summer		Autumn	
	$\bar{x}$	S	U-test	S	U-test	S	U-test	S	U-test
Canopy cover (%)	55.8	<	0.001	<	0.001	<	0.001	<	0.001
Spruce (%)	73.1		n.s.	>	0.001	>	0.001	>	0.001
Fir (%)	15.3	>	0.05		n.s.		n.s.		n.s.
Beech (%)	9.6		n.s.	<	0.001	<	0.001	<	0.001
Other deciduous (%)	1.2	<	0.01	<	0.001	<	0.001	<	0.001
Diversity index	5.2		n.s.	<	0.001	<	0.001	<	0.001
Vegetation layers	2.3		n.s.	<	0.001	<	0.01	<	0.001

Selection (S) (variable in locations <, > expected) was tested (U-test) comparing locations to availability on Teisenberg ($\bar{x}$)

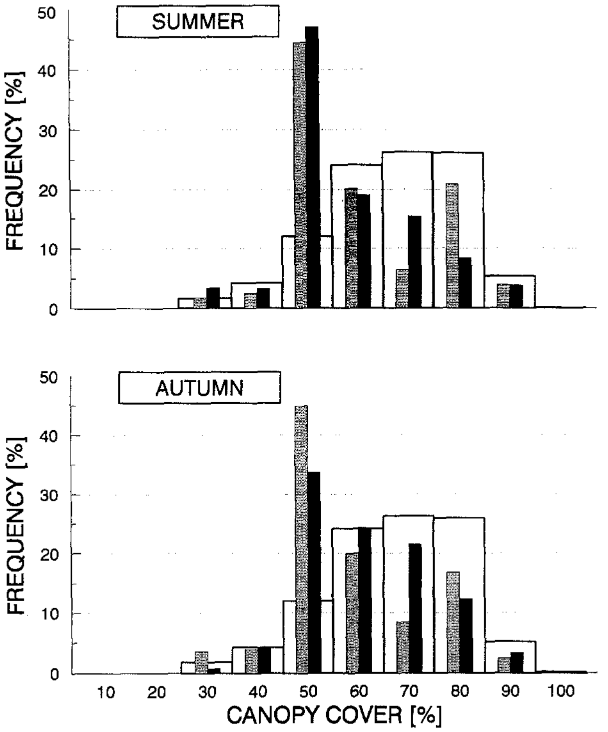

Fig. 4. Distribution of summer and autumn locations of hens (*grey*; $n = 437$ and 535, respectively) and cocks (*black*; $n = 1501$ and 1305) in pole-stage and older forest, in relation to canopy cover of various density. Canopy cover in pole stage averaged 75 ± 11% ($\bar{x} \pm$ SD), middle-aged forest: 70 ± 10%, old forest: 56 ± 11%

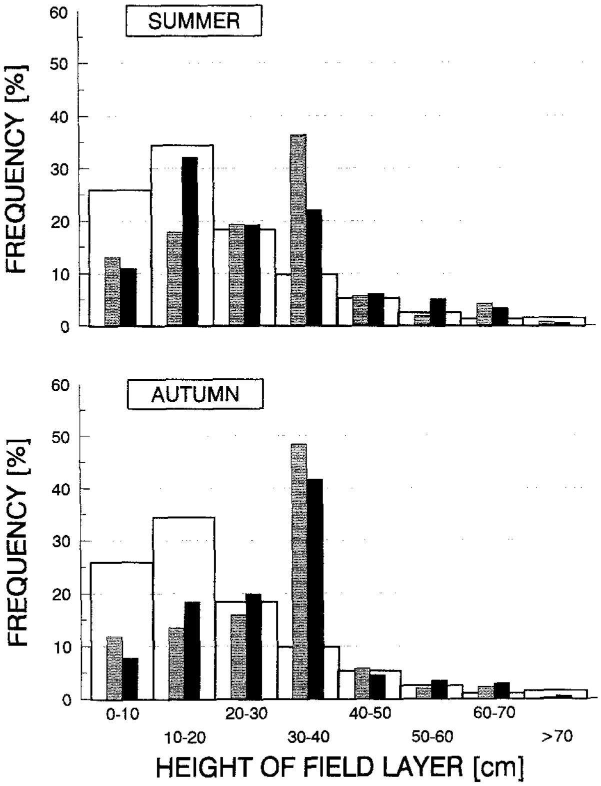

Fig. 6. Availability of ground vegetation of various heights (% of total area; *open columns*), and distribution of hen *(grey)* and cock *(black)* locations in summer and autumn

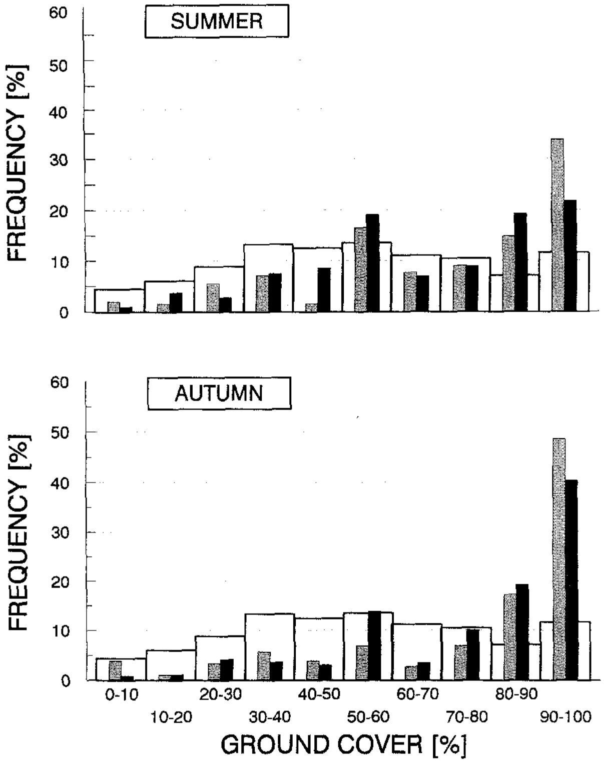

Fig. 5. Distribution of hen *(grey)* and cock *(black)* locations in relation to availability of ground cover (% of total area; *open columns*)

($r = -0.35$, $P < 0.001$, old forest), and the birds used old forest with fewer vegetation layers than expected (Table 4).

Capercaillie selected sites with higher ground coverage (*U*-tests, $P < 0.001$ for both sexes and seasons) (Fig. 5) and taller vegetation (*U*-tests, $P < 0.001$ for both sexes and seasons) than expected. In summer, cocks used shorter vegetation (*U*-test, $P < 0.01$) (Fig. 6), and in summer and autumn, they used stands with less ground cover (*U*-tests, summer: $P < 0.001$, autumn: $P < 0.05$) than hens.

Capercaillie preferred locations with high proportions of bilberry (*U*-tests, $P < 0.001$ for either sex and season) (Fig. 7), and avoided all other vegetation types (Fig. 8). In old forest, this resulted in lower scores of diversity of ground vegetation than expected (*U*-tests, $P < 0.001$ for either sex and season). Hens used middle-aged and pole-stage habitats randomly in relation to diversity of ground vegetation types, and preferred clearcuts and thickets with high diversity scores (*U*-tests, $P < 0.001$ for both habitats and seasons). Cocks selected ground vegetation with high diversity in all habitats younger than old forest (*U*-tests, $P < 0.05$ in all habitats and both seasons). However, in all stages younger than old forest, bilberry cover and diversity were positively related ($r = 0.2$–0.4, $P < 0.05$ for all habitats).

Capercaillie used sites with more anthills than expected (*U*-tests, $P < 0.001$ for either sex and season, all hab-

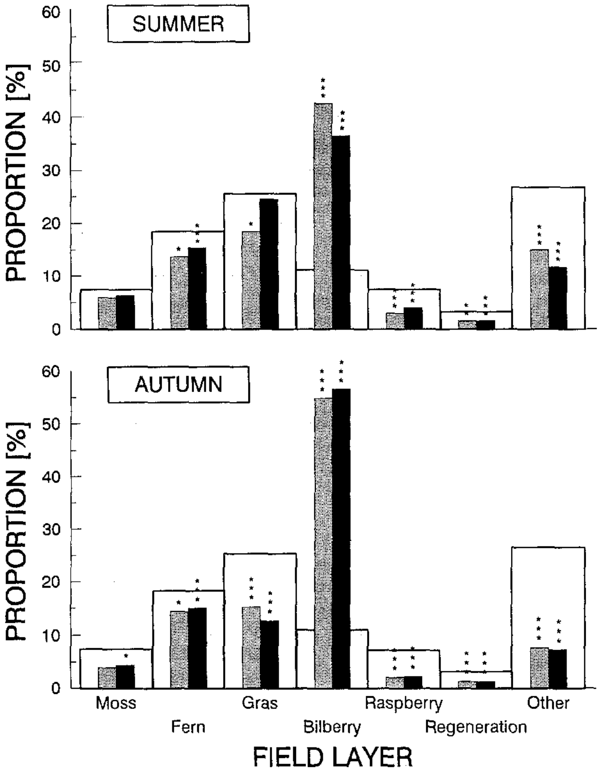

Fig. 7. Proportions (%) of various types of ground vegetation in old forest (% of total area; *open columns*), and distribution of hen (*grey*; $n=248$, summer, and 324, autumn) and cock (*black*; $n=585$, 747) locations (see Table 1 for definition of vegetation types). *Asterisks* indicate significant differences from random distribution (*U*-test, * $P<0.05$, ** $P<0.01$, *** $P<0.001$)

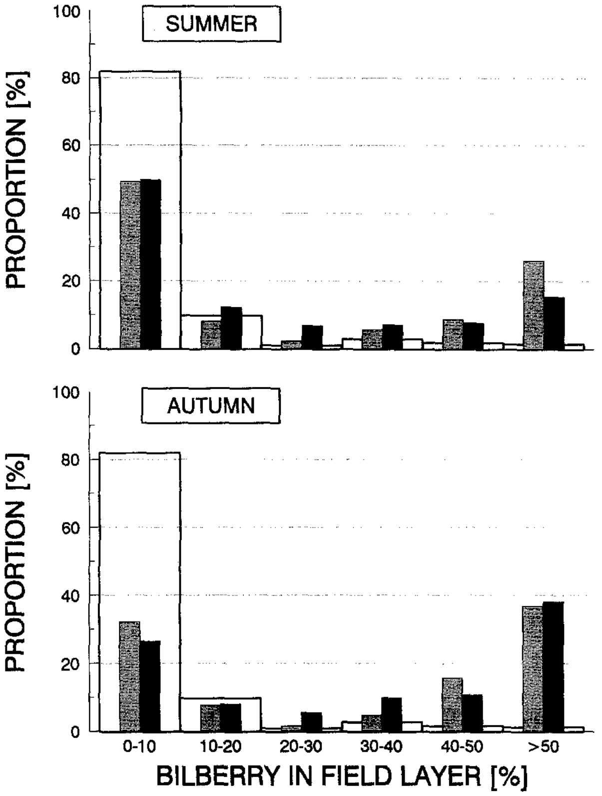

Fig. 8. Distribution of bilberry in the field layer (% of total area; *open columns*), and distribution of hen *(grey)* and cock *(black)* locations

itats pooled). Also, within old forest, they selected stands with high frequency of anthills (*U*-tests, $P<0.001$ for either sex and season). However, occurrence of ants was positively linked to bilberry cover (all habitats: $r=0.26$, $P<0.001$; old forest: $r=0.33$, $P<0.001$).

Selection of summer home ranges

As no age-related differences in home range size were evident, I pooled all capercaillie age classes. Hens had smaller summer home ranges [162 ± 106 ha ($\bar{x} \pm$ SD), $n=13$] than cocks [248 ± 142 ha, $n=38$) ($t=2.0$, $P=0.05$), and selected ranges with high proportions of old forest (Fig. 9). Range size was negatively related to old forest ($r=-0.48$, $P=0.10$) and to mean bilberry cover ($r=-0.40$, $P=0.18$). A multiple regression with old forest and bilberry as independent variables revealed a negative relation with home range size ($R=0.51$, $F=1.75$, $df=2$, 10, $P=0.22$). Due to limited sample size, none of these relations was significant however. Within their home ranges, hens used habitats other than old forest less than expected (Fig. 9). Habitat composition of home ranges of cocks was similar to expectation, but within their home ranges, they preferred old forest (Fig. 9). Male range size was independent of the amount of old forest ($r=-0.06$), but was negatively related to mean bilberry cover ($r=-0.38$, $P<0.01$) within the range.

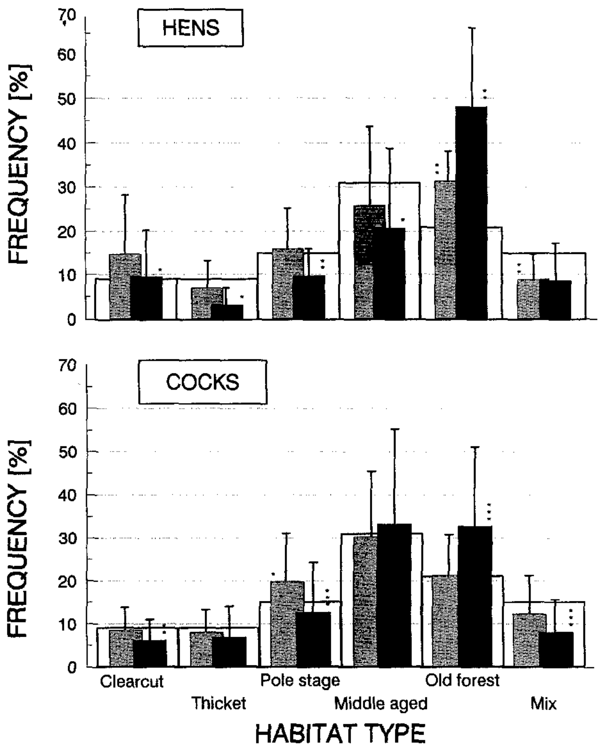

Fig. 9. Habitat types in the study area *(open columns)*, in summer home ranges (*grey*; $\bar{x} \pm$ SD), and at locations within home ranges (*black*; $\bar{x}+$SD). *Asterisks* indicate differences between use and availability; above *grey columns*: home ranges vs. study area; above *black columns*: locations vs. home ranges (Wilcoxon test, * $P<0.05$. ** $P<0.01$, *** $P<0.001$)

Discussion

Habitat selection at the landscape scale

My study showed that in the Alps as in other areas capercaillie habitat is generally characterized by late stages of forest succession (reviews by Klaus et al. 1986; Leclerq 1987; Rolstad and Wegge 1989). As repeatedly reported from mountainous areas (see review in Klaus et al. 1986), selection of habitats at the landscape level appeared to depend on topography. However, in many cases this may result from habitat structure rather than topography *per se*. On Teisenberg, the distribution of bilberry explained the distribution of capercaillie in relation to altitude and exposure throughout the year (Storch 1993a). Gentle slope seems to be a general feature of alpine capercaillie habitats. Avoidance of steep slopes has been previously noted (Eiberle 1976; Zeimentz 1981), and was evident in winter (Storch 1993b), spring (Storch 1993a), and autumn on Teisenberg, but was less pronounced in summer.

High amount of edge is frequently considered a significant feature of central European capercaillie habitats (e.g. Stein 1974; Klaus et al. 1985). In contrast, in this study capercaillie preferred large patches and showed no preference for edge-rich old forests on Teisenberg. In relatively dense surroundings, edges may offer better cover and food than the adjacent forest, and may be frequented by capercaillie. However, edges are preferred hunting sites of the goshawk *Accipiter gentilis* (Widén 1985), an important predator of capercaillie (Wegge et al. 1990; Storch 1993a). I conclude that edge is not a critical feature of capercaillie habitat, as long as canopy closure allows rich herbaceous growth within the forest. As indicated by their selection of large old forest patches and small clearcuts, capercaillie prefer a landscape mosaic similar to pristine boreal forest (Hansson 1992), the environment in which they evolved.

Habitat structure

Capercaillie prefer moderate canopy coverage of about 50% (Gjerde 1991; Storch 1993b; this study). Such forests offer enough space to fly in, and provide luxurious ground vegetation. On Teisenberg, this corresponds best with old forest, although even within this habitat type, I recorded selection towards open structure. My results demonstrate that about two-thirds of the pole stage and older forests on Teisenberg were too dense to be optimal capercaillie habitat. The situation is probably very similar throughout the Bavarian Alps.

In contrast with the frequently repeated opinion that capercaillie in central Europe require multilayered forests of high diversity (e.g. Glutz von Blotzheim 1973; Scherzinger 1974; Klaus et al. 1985; Leclercq 1987), Teisenberg birds preferred neither high diversity of tree species, nor multilayered old forest stands. I suspect that these are not features capercaillie select directly, but that rather in some areas they may be related to habitat factors preferred by the birds.

Capercaillie selected sites with a well-developed field layer. Due to the overwhelming preference for bilberry, they did not generally select high species diversity in the understory. The birds rarely used vegetation taller than 40 cm, which would not allow them to watch for predators. Due to their smaller size, hens suffer higher predation than cocks (Wegge et al. 1990; Storch 1993a). During the snow-free season, hens seem to avoid predation by hiding in the ground vegetation (Rolstad et al. 1988). In contrast to hens, the cocks' strategy is to detect and watch a predator and escape or fight (Rolstad et al. 1988; own observations). They rely on concealing cover less than hens, and use sites with incomplete cover and short ground vegetation. Distinct predator avoidance strategies, especially during the moult in summer, may explain why hens were more closely bound to old forest than were cocks.

The importance of anthills for capercaillie is another impression frequently repeated in central European literature (e.g. Glutz von Blotzheim 1973; Müller 1974; Klaus et al. 1986). My results revealed that adult capercaillie, like broods (Storch 1993a), used habitats with more anthills than expected. On Teisenberg, ants never reached more than 6% and 2% per month in the diet of hens and cocks, respectively (Schwarzmüller 1990). As the occurrence of anthills and bilberry were intercorrelated, the strong preference for bilberry-rich ground vegetation may be the primary explanation why anthills are common in habitats selected by adult capercaillie.

Selection of home ranges

The negative relation between bilberry cover and size of individual home ranges further underlined the importance of bilberry in capercaillie summer habitats. Hens preferred old forest both for home ranges and sites within home ranges, and range size seemed to vary with the amount of old forest. The proportions of habitat types in ranges selected by cocks were similar to availability in the study area, and the preference for old forest was largely due to selection within home ranges. Taking into account the different methods used for home range estimation, summer ranges were comparable in size on Teisenberg and in the boreal forest of Norway (Rolstad et al. 1988).

Intersexual niche segregation?

Capercaillie are the largest and most dimorphic grouse species. Fennoscandian studies reported evidence of intersexual niche segregation due to size dimorphism. Seiskari (1962) first pointed out niche segregation in winter, with cocks associated with old forest, while hens preferred denser habitats of young successional stages. Comparing cocks and broodless hens, Rolstad et al. (1988) confirmed this pattern for the summer in the boreal forest, while in autumn, both sexes showed affinity for old forest (Rolstad 1988).

My results contradict the hypothesis of intersexual niche segregation. Although the distribution of hens was more closely related to ground cover, habitat distribution of the sexes completely overlapped in relation to all factors studied. In contrast to the Fennoscandian findings mentioned above, both sexes clearly preferred old forest throughout the year (Storch 1993b; this study). Boreal and central European coniferous forests differ markedly in species composition and productivity, and thus in habitat structure. Therefore, successional stage is not a sufficient measure to describe capercaillie habitat throughout its range.

In central Europe, young successional stages of spruce-dominated forests are dense, and ground vegetation is sparse until beyond the second thinning. The capercaillie's preference for a well developed understory (Klaus et al. 1986; this study) explains the pronounced avoidance of young forests in the Alps. In the boreal forest, however, young seral stages offer sufficient ground cover to capercaillie (Rolstad et al. 1988). My results agree with the notion that, due to their smaller size, hens are able to utilize denser forests than cocks (e.g. Klaus et al. 1986; Rolstad et al. 1988). However, at least during summer and autumn, they will not frequently do so unless a well developed field layer is present.

Seasonal differences

Habitat selection by capercaillie showed the same patterns in summer and autumn. However, there were some trends due to phenology and spacing patterns of capercaillie. Bilberries ripen in August, and reach a peak in the capercaillie diet in September (Storch et al. 1991). As the best bilberry sites are distributed in a clumped pattern, capercaillie concentrate in these habitats in autumn. Correspondingly, the association with bilberry grew stronger from summer to autumn. In addition, this was supported by the autumn movements of cocks back to the leks, which were situated in bilberry-rich old forest areas (Storch 1993a). Therefore, the use of old forest also increased. These results were in accordance with the findings of Rolstad et al. (1988) in Norway.

The role of bilberry

In view of the wide array of foods in the summer diet of capercaillie (Jacob 1987; Storch et al. 1991), the close association with bilberry is striking. Bilberry provides high-energy food and suitable cover to the capercaillie. These are not exclusive properties of bilberry, and may be substituted by other ground vegetation. Capercaillie feed on other berries, but these either do not provide cover (strawberry *Fragaria* spp.) or can hinder the birds' movements (raspberry, blackberry *Rubus* spp.). Seeds of grasses also provide nutritious food, but grasses grow late and wither early, and therefore provide cover only during part of the season. In contrast to all other types of ground vegetation, bilberry provides optimal food and cover throughout the snow-free season. Due to this complete overlap of resources in time and space, high availability of bilberry will enable capercaillie to minimize movements in search of food and cover, resulting in limited home range size, and therefore may reduce the risk of predation. On Teisenberg, survival was generally high however (Storch 1993a), and did not allow a test for a relation between bilberry cover and survival of individuals.

Due to the omnipresence of *Vaccinium,* studies in the boreal zone fail to evaluate the role of bilberry in habitat selection by capercaillie, especially on the landscape scale. In the limestone zone of the Alps, bilberry is sparse and patchily distributed, both on the local and landscape scale. Due to acidic soils, the conditions are more favourable in the foothills, but there also, bilberry occurs patchily.

My study revealed a convincing association of capercaillie and bilberry at all levels of spatial scale. Nevertheless, capercaillie may inhabit forests where bilberry is sparse or absent, as observed in many areas of the Alps. Bilberry is not necessarily a factor limiting capercaillie distribution, as habitat selection may be density-dependent. Present-day density of capercaillie in the Alps is low as indicated by bag records and hunting reports from the past centuries. Following the ideas of Fretwell and Lucas (1970) and Fretwell (1972), I suspect that at low population densities capercaillie will concentrate in optimal habitats, namely those with luxuriant bilberry cover, as observed in this study. As numbers grow, predation risk may increase and thereby, in terms of individual fitness, may lower the quality of the optimal habitats. The population then should spread out and increasingly use suboptimal habitats. As Rosenzweig (1985) concluded, the quality of habitats will be easiest to assess by comparing their utilization patterns when a species is rare. Ranking of habitats will be more transparent when a species is common. The latter points to the shortcoming of my study: it became quite clear that luxuriant bilberry cover is the capercaillie's best choice. However, the second best remains uncertain.

As mentioned earlier, there is growing concern about vegetation changes due to eutrophication of grouse habitats in central Europe (Porkert 1982; Ellenberg 1983; Klaus et al. 1985; Biedermann 1992; Ellenberg 1992). Loss of bilberry in favour of grasses may lead to reduced availability of insect food (Biedermann 1992) and cover for chicks, and hence may affect reproductive success of capercaillie (Storch 1993a). Furthermore, as my study demonstrates, loss of bilberry will certainly result in reduced habitat suitability for adult capercaillie, and will thus contribute to population decline.

Acknowledgements. I am greateful to the many students who helped with habitat mapping and telemetry. Heiko Liedeker's expertise was of invaluable help with GIS data processing. Ulrich Hehl drew the figures. Thanks to Jon Swenson and to two anonymous referees for comments on the manuscript. Financial support was received from the Bavarian State Ministry of Agriculture and from IBM Germany.

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