Male territoriality, female range use, and spatial organisation of capercaillie Tetrao urogallus leks

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Ilse Storch

This paper compares spacing behaviour of male and female capercaillie *Tetrao urogallus* in the German Alps, to those reported from the boreal zone, and discusses their implications for models of lek evolution. Based on 23 males and 13 females radio-tracked during April-May 1988-1992, the size, arrangement, and overlap of home ranges of males, and home ranges, lek visitation, and location of nest sites of females are described in relation to habitat, lek location, and the birds' age. Independently of sex and age, capercaillie preferred old forest habitats. With the exception of juveniles and some subadults that used large home ranges and visited several leks, males occupied permanent but overlapping territories clumped within 1 km of lek centres. Territorial traits were most pronounced in the oldest, dominant males: they used the smallest territories closest to the lek centre, used the central parts of their territories exclusively and showed the strongest site tenacity; nevertheless they tolerated subordinates within their territories. Females stayed farther from leks than males, most visited several leks, and nested at random distances from leks. Independently of habitat, multi-lek females used larger home ranges than single-lek females. The great variation in female home range size did not agree with Bradbury's hotspot and female-preference hypotheses, indicating that female home range size may be unsuitable in revealing clues about lek evolution in capercaillie.

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Grouse, Tetraoninae, have received special emphasis in studies of sexual selection and the evolution of mating systems. The forest-dwelling capercaillie *Tetrao urogallus*, the largest and sexually most dimorphic grouse, has been hard to classify (Wiley 1974, Wittenberger 1978, de Vos 1979, Johnsgard 1983) among species with dispersed versus clumped polygamy, or leks (*sensu* Bradbury 1981, Höglund & Alatalo 1995). Its mating system may be regarded as transitional between the typical dispersed territoriality of other forest grouse, such as the spruce grouse *Dendragapus canadensis*, which display solitarily within permanent territories, and true lek-forming species, such as the black grouse *Tetrao tetrix*, which are territorial on but not off the lek.

In Scandinavia, capercaillie males were reported to establish permanent spring ranges clumped around lek centres, where display activity is most intense (Hjorth 1970, de Vos 1979, Wegge & Larsen 1987); the oldest males occupy largely exclusive 20-30 ha territories closest to the lek centre and experience the highest mating success, whereas juveniles and most subadults are non-territorial using larger ranges farther from the lek centre which may overlap the territories of adults (Wegge & Larsen 1987). Most females apparently visit a single lek and mate with the same, high-ranking male (Hjorth 1970, Wegge & Larsen 1987).

The behaviour of females is believed to play a central role in the evolution of lek mating systems. In particular, female home range size in relation to lek spacing has been suggested to provide a means for

distinguishing between alternative models of lek evolution: according to the 'hotspot' model, males cluster in locations preferably used by females and leks are more closely spaced than the diameter of female home ranges; in the 'female preference' model, females prefer aggregations of males and leks are at least one female home range apart (Bradbury 1981, Bradbury & Gibson 1983, Bradbury, Gibson & Tsai 1986).

On Teisenberg, males aggregate within a 1-km radius from their home-lek throughout winter and spring, move to distinct summer home ranges in June, are dispersed within a 3-4 km radius during summer, and return to their leks in autumn (Storch 1995). There are no pronounced seasonal movements in females; their summer and winter home ranges overlap, and throughout the year they are dispersed within a radius of 3 km from the lek they attend in spring (Storch 1995). Females occupy their breeding home ranges from March throughout summer and autumn. Throughout the year old forest is the habitat type preferred by males and females (Storch 1993 a,b, 1994). During April and May, both sexes gradually change from a winter diet consisting of conifer needles to increasing amounts of herbaceous plants (Storch, Schwarzmüller & von den Stemmen 1991).

To date we do not know whether the spacing patterns described from Scandinavian capercaillie leks also apply to central European populations. Therefore, the main objective of this paper is to report on the spacing of capercaillie in the Alps and to compare these results to the findings from the boreal forest. I examined spacing and territoriality of males and describe size, arrangement, and overlap of home ranges in relation to habitat, lek location, and age of bird. I show that territorial traits were most pronounced among the oldest males, that nevertheless, tolerated subordinates within their territories. I examined range use of females and describe home ranges, lek visitation, and location of nest sites in relation to habitat and spacing of leks. Based on the results, I agree with Wegge & Larsen (1987) that neither Bradbury's hotspot nor the female-preference hypothesis of lek evolution (Bradbury 1981, Bradbury & Gibson 1983) are supported by data on capercaillie.

Methods

Study area

The foothills of the Bavarian Alps, Germany, are characterised by extensive coniferous and mixed forests. Forestry practices have formed a mosaic of stands of various size and age. I studied the capercaillie population in the Teisenberg area (50 km²; 47°48'N, 12°47'E), a mountain range with elevations from 700 m a.s.l. in the valleys to 1,300 m a.s.l. in the central part to 1,800 m a.s.l. in the south. The treeline varied between 1,300 and 1,500 m in altitude. Capercaillie used almost exclusively the upper slopes between 1,000 and 1,300 m altitude. The climate is moist and temperate, and during the years of study, snow depth at capercaillie leks varied between 0 and 1.5 m in early May.

The Teisenberg forests were dominated by Norway spruce *Picea abies* (70%), intermixed with beech *Fagus sylvatica* (15%) and fir *Abies alba* (10%). Forest stands ranged in size between 1 and 100 ha and were distinguished as: 1) clearcuts (cleared areas covered by natural regeneration), 2) thickets (young forest before thinning), 3) pole stage (after first thinning, mean canopy cover 75%; app. 20-50 years old), 4) middle-aged forest (after second thinning, mean canopy cover 70%, sparse ground vegetation, app. 50-90 years), and 5) old forest (final felling stage, mean canopy cover 56%, rich ground vegetation, ≥90 years). Uneven-aged stands with small scale (<1 ha) variation in age were described as 'mixed' when no stage comprised ≥75% of the area. Storch (1993a) gives details regarding habitat mapping.

Capturing and radio telemetry

Using mist nets, I caught 13 female and 23 male capercaillie in autumn in preferred habitats rich in bilberry *Vaccinium myrtillus*, and in spring (mostly April) at the two largest leks and off the leks (>500 m from a lek centre). Based on the primary feathers I distinguished juvenile (≤1 year) and adult females (Helminen 1963). Based on beak depth measured to the nearest 0.5 mm, I aged males as juveniles (≤1 year old), subadults (>1-3 years old), adults (>3-5 years old), and older adults (>5 years old) (Storch 1993a). Males captured as adults were classified as older adults after two years of study. Birds that were tracked for several years were included in the analyses only once per age class.

I marked the birds with necklace transmitters with life expectancy of two years. The radios weighed 28 g for females and 35 g for males, i.e. 0.8-1.4% of the body weight. The transmitters were completely hidden beneath the birds' plumage, and did not notably affect behaviour. In April and May, 1988-1992, the

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birds were located by triangulation using a portable receiver and a 4-element yagi-antenna. Most bearings were taken from forest roads at distances of <500 m. Typically 4-6 bearings were taken per fix. Consecutive locations were separated by at least 12 hours (see Storch (1993a) for details on telemetry). A total of 570 female and 1,675 male radio locations with error polygons <5 ha were used to analyse home ranges and spacing in the period from 1 April to 31 May; habitat selection was analysed using 313 female and 1,461 male radio locations with error polygons <1 ha. The nest sites of radio-tagged females were determined during incubation, i.e. during May-July. This study indicated great individual variation in female mobility in spring; in order to assess whether similar differences occurred also in other seasons, I re-analysed data on winter (December-March; Storch 1993a), summer (June-August; Storch 1993b) and annual (Storch 1995) home ranges of the individuals tracked in spring.

Estimation of home ranges

In order to assess habitat selection and spacing of females and males I defined a home range as the total area cruised by an individual, calculated as 100% convex-polygons. Based on five birds for which >60 locations had been obtained during the 61-day period of April and May, 20 locations will result in 80%, 30 in 90%, and 40 in 95% of the size of a range based on 60 locations. Therefore, home range size and width of both sexes and home range overlap and tenacity in males was calculated for home ranges based on ≥25 locations evenly distributed over the period from 1 April to 31 May; numbers of locations were 42 ± 16 ($\bar{x}$ ± SD) in males and 40 ± 14 in females. When calculating distance of locations from leks and assessing habitat composition within home ranges, home ranges based on ≥15 locations were included, because there were no differences in distance from leks and habitat composition between home ranges based on 15-24 and those based on ≥25 locations.

In lek evolution models, the size of female pre-breeding home ranges is used as an indicator of female mobility. Beehler & Foster (1988) criticised this approach because of the difficulty of defining a home range; at least in some lekking species, including the capercaillie (Wegge & Rolstad 1986), females travel outside their normal ranges in order to visit leks. To test the predictions of the female-preference and hotspot models of lek evolution (Bradbury 1981, Bradbury & Gibson 1983), female home ranges were

calculated from 1 April to the beginning of incubation or to 31 May if incubation started later, excluding visits to leks at times when males were present. Therefore, female locations at <500 m distance from the lek centre, obtained between 17.00-09.30 hours (the time most males spent close to lek centres) from 15 April to 15 May, were excluded from home range calculations.

From late afternoon to the end of morning display, males stayed close to the lek centre; during daytime, they used, mainly but not exclusively, the outer parts of their home ranges. Therefore, total home ranges (all locations from April and May) may be subdivided into display and daytime ranges (Wegge & Larsen 1987). On Teisenberg, males left their display ranges mainly between 09.00 and 10.00 and returned after 16.30; the sun rose between 05.45 and 04.15, and set between 18.40 and 20.00 CET on 1 April and 31 May, respectively. To compare spacing of males in relation to time of day, I distinguished between the periods from 10.00-16.30, termed daytime period, and from 17.00-09.30, termed display period. This terminology does not imply that male activities were strictly split in time and space: display activity was neither fully restricted to the evening and morning hours nor to lek centres, and to some extent lek centres were used throughout the day and for non-mating activities as well. For display and daytime ranges only locations obtained from 1 April to 15 May were included, when leks were regularly attended by the birds (1989-1992). For 1988, when display ceased two weeks later than in the other years, the period from 15 April to 31 May was considered. Analyses of male home range size and distance from leks included only those daytime ranges and display ranges that were based on ≥15 locations; mean number of locations was 20 ± 7 ($\bar{x}$ ± SD) for display and 19 ± 5 ($\bar{x}$ ± SD) for daytime ranges. This definition may underestimate home range size to some degree; the main purpose, however, was to compare between age classes rather than to provide exact figures on home range size.

Analysis of habitat use

Habitat availability was calculated using the upper slopes of Teisenberg (subsequently referred to as the study area), the range in altitude used exclusively by capercaillie in spring. To assess habitat availability, I measured the proportions of forest stages within the study area, within individual home ranges, and within circles of 800 m radius around lek centres, where

most males have their display and daytime ranges (Wegge & Larsen 1987, this study).

All variables were tested for normality, and parametric vs non-parametric statistics were selected accordingly.

I assessed habitat use comparing the distribution of radio locations with the availability of forest stages within the study area (χ^2-test; Bonferroni z-test, Neu, Byers & Peek 1974). To test for individual variation in habitat preferences, I compared the proportion of radio locations in old forest with the proportion of old forest in the study area (Wilcoxon signed-rank matched-pair test).

To assess selection and use of home ranges, I compared the proportions of old forest in home ranges and in the study area (Wilcoxon signed-rank matched-pair test), and compared the relative use of old forest (U), measured as the proportion of individual locations in old forest, with availability (A) of old forest within each home range. I calculated Ivlev's electivity index (Krebs 1989) as $I = (U - A) / (U + A)$, and tested observed electivity scores versus random utilisation ($I = 0$) (Wilcoxon signed-rank matched-pair tests). ANOVA and t-tests were used to assess age-related differences in range use, and Pearson's correlation coefficients and Mann-Whitney U-tests to evaluate the relation between habitat factors, home range size, and survival.

Analysis of spacing patterns

For each year, I calculated the geographical centres of leks 1 and 2 as the arithmetic mean of all locations of all males that used a well-defined range at a single lek, obtained from 17.00-09.00 between 15 April and 31 May 1988, and 1 April and 15 May 1989-1992, respectively. For the smaller leks 3 and 4, data from all years were pooled. I estimated the number of males per lek based on telemetry and direct observations.

To analyse spacing in relation to the lek, I measured the mean distance of locations of individuals to the centre of the lek they used most frequently, and tested for sex-, time-of-day (t-test, Mann-Whitney U-test), and age-related differences (ANOVA).

In this paper, I use the term home range in an inclusive way, and define a territory as a home range that is exclusively used or defended. To evaluate male territoriality, I estimated the mean proportion of overlap between neighbouring male daytime and display ranges, calculated as 100, 75, and 50% convex polygons. I assessed site tenacity by the proportion of the area of a male's home range in year$_{t+1}$ already used the previous year, i.e. overlapped by his home range in year$_t$. Age-related differences in territoriality were evaluated using Mann-Whitney U-tests and t-test.

I defined a female as visiting a lek when she was located during the morning display hours (05.00-09.30) in the periods 1-31 May 1988 or 15 April to 15 May 1989-1992 within a radius of <500 m from the lek centre, i.e., where most adult and older males had their display ranges. I distinguished single-lek and multi-lek females, depending on the recorded number of leks visited within the same season, and compared spacing patterns between these groups by t-tests. To test whether multi-lek females were generally more mobile than single-lek females, I compared the sizes of winter, summer, and annual home ranges of the same individuals tracked during spring (U-test, Wilcoxon rank sum W-test).

To address Bradbury's hypotheses on lek evolution, I compared inter-lek distances with home range diameters and with distances from nest sites to the lek a hen most frequently attended (t-tests, Mann-Whitney U-tests). Furthermore, I generated random points within the Teisenberg area equal to the number of nest sites, and compared their nearest-lek distances with those of nest sites (Mann-Whitney U-test).

Direct observations of the behaviour of capercail-

Table 1. Availability of habitat types (% total area) and utilisation (% radio locations) by female and male capercaillie on Teisenberg, Bavarian Alps, and P-values according to Bonferroni z tests (availability vs utilisation). Display: 17.00-09.30; daytime: 10.00-16.30; for females, all locations were pooled.

				Utilisation			
						Males	
	Availability	Females		Display		Daytime	
Habitat type	(%)	(%)	P <	(%)	P <	(%)	P <
Clearcut	6.9	10.4	0.05	6.1	n.s.	9.5	0.01
Thicket	12.6	5.4	0.001	2.3	0.001	3.8	0.001
Pole stage	20.8	11.1	0.001	6.8	0.001	9.9	0.001
Middle aged forest	30.1	21.5	0.001	22.9	0.001	27.8	n.s.
Old forest	17.2	44.9	0.001	53.1	0.001	41.1	0.001
Mix	12.5	5.7	0.001	8.7	0.001	7.9	0.001

lie, made at leks, are reported where they may provide additional clues for interpreting the data, however, they were not made in a systematic way that would allow quantification.

Results

Habitat selection

Females ($\chi^2 = 200$) and males ($\chi^2 = 1,013$; df = 5, P < 0.001 for both) used forest stages non-randomly, and preferred old forest (Bonferroni z-test, P < 0.001 for both) (Table 1), a preference that was uniform among individuals (females z = -3.18, N = 13, P = 0.002; males z = -4.23, N = 32, P < 0.001; Wilcoxon test). As females used habitats similarly during day and night ($\chi^2 = 8.2$, df = 5, P = 0.14), all locations were pooled. Males used old forest more frequently ($\chi^2 = 26.6$; df = 1, P < 0.001) at times they generally spent in display ranges than in daytime ranges. Differences in habitat use between the sexes ($\chi^2 = 15.5$, df = 5, P < 0.01) were due to less use of middle-aged forest by females than by males (Bonferroni z-test; P < 0.05); during daytime, males used middle-aged forest according to its availability.

Both sexes used home ranges with proportions of old forest (females 35.5 ± 20.0% ($\bar{x}$ ± SD), N = 13; males 31.3 ± 20.3%, N = 32) larger than the average availability in the study area (17.2%) (females z = -3.11, P = 0.002; males z = -3.24, P = 0.001); the proportions of old forest in male home ranges also exceeded availability of old forest within an 800-m radius around lek centres (Table 2) (z = -2.39, P = 0.017). The frequency of radio locations in old forest
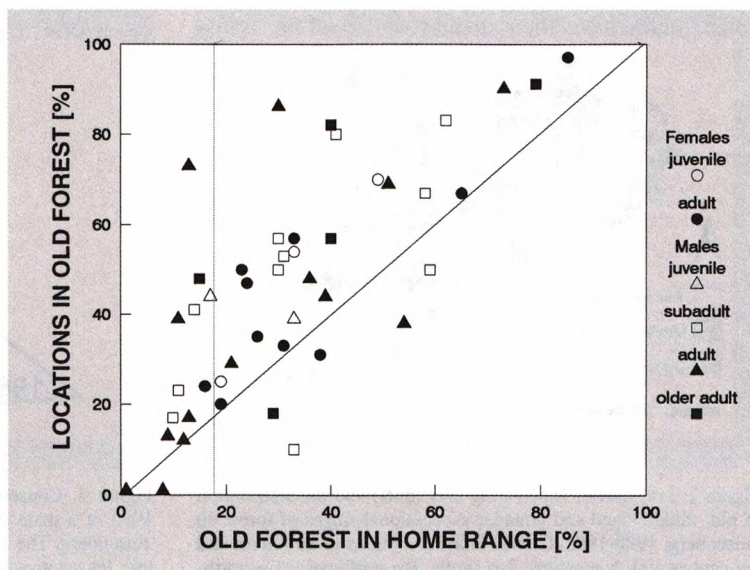

Figure 1. Proportion of old forest in the home ranges and radio locations of individual capercaillie on Teisenberg, April - May 1988-1992. The diagonal line indicates random use of old forest within home ranges; the vertical dotted line indicates the proportion of old forest in the study area (17%).

(females: 46.9 ± 22.1% ($\bar{x}$ ± SD); males: 45.8 ± 27.1%) was higher than the availability within the individual home ranges (females z = -2.83, P = 0.005; males z = -2.53, P = 0.010) (Fig. 1). In males, both the preferences for home ranges (F = 0.74, df = 3, 28, P = 0.54) and for locations (F = 0.64, df = 3, 28, P = 0.59) rich in old forest were independent of the birds' age. During spring, four males were killed by predators. Males that died had less old forest in their home ranges (11 ± 7% ($\bar{x}$ ± SD), N = 4) than those surviving (36 ± 20%, N = 26; U = 14.0, P = 0.018).

Spacing of leks and males

Four leks (≥2 displaying males) were known on Teisenberg, and all were used by radio-tagged birds (Fig. 2, Table 2). Calculated lek centres represented

Table 2. Aspects of lek attendance and forest fragmentation from Teisenberg leks, Bavarian Alps, 1988-1992. Displaying males estimated based on telemetry and direct observations; as an index of female lek attendance, the total number of radio-tagged females recorded visiting the lek in 1988-92 was used.

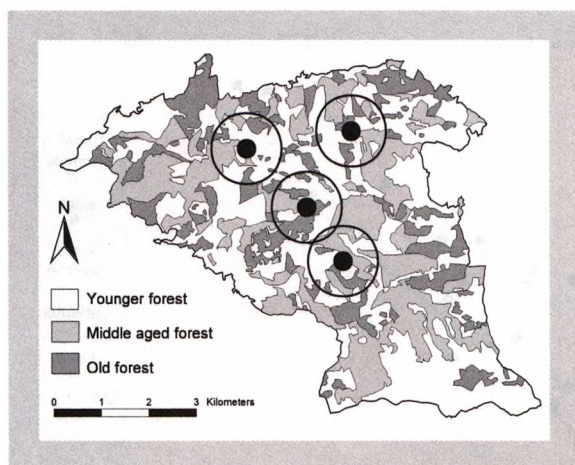| Variable	Lek 1	Lek 2	Lek 3	Lek 4
Males displaying (N)	15-20	3-6	2-3	2-3
Females visiting (N)	13	6	1	2
Habitat within 400 m from lek centre				
Old forest ha (%)	30 (60)	12 (24)	17 (34)	4 (8)
Old and middle aged forest ha (%)	37 (74)	27 (54)	22 (44)	16 (32)
Habitat within 800 m from lek centre				
Old forest ha (%)	60 (30)	28 (14)	36 (18)	30 (15)
Old and middle aged forest ha (%)	100 (50)	96 (48)	70 (35)	76 (38)

Figure 2. Location of capercaillie leks (dots) and the distribution of old, middle-aged and younger successional stages of forest on Teisenberg, 1988-1992. Circles indicate a radius of 800 m around lek centres; lek 1 = centre, 2 = south, 3 = north-east, 4 = north-west).
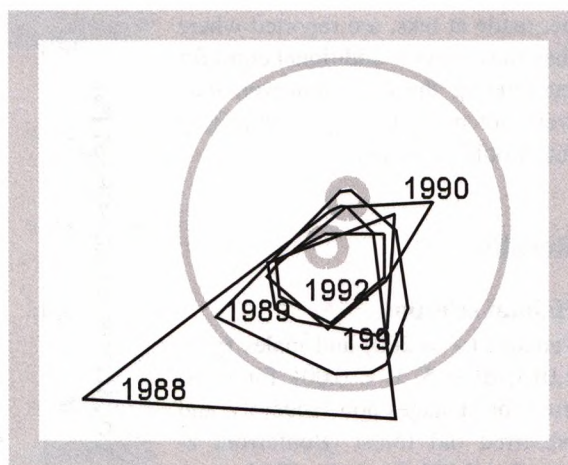

Figure 4. Consecutive spring home ranges in April-May 1988-1992 of a male capercaillie (two years old in 1988) at lek 1 on Teisenberg. The large circle indicates an 800-m radius around the lek; lek centres shifted between years and are indicated by the small circles (above: 1988-89, below: 1990-92).

the areas of the highest display activity well. These were not fixed; the centre of the largest lek shifted by 50, 270, 120, and 50 m between successive years. On average (1988-1991), the centres of neighbouring leks were 1.3 (leks 1-2), 1.9 (1-4), 2.0 (1-3), and 2.4 (3-4) km ($\bar{x} \pm$ SD = 1.9 $\pm$ 0.5 km) apart. Proportions of old forest were higher in the central than in the outer parts of the lek areas. The number of males per lek seemed to be associated with availability of old forest (see Table 2); the small sample of leks did not allow further analysis, however.

All males attended leks. No adult or older male vis-

ited more than one lek, or changed leks, during the 28 bird seasons observed. In 15 subadult seasons observed, two males visited two leks in the same season, and one changed from lek 1 to lek 2 at the age of three. One juvenile explored an area of at least 25 km², and visited all four leks in his first spring (March-May). The next year, he settled at lek 2, the lek closest to where he had spent his first summer. The other juvenile stayed at lek 1, however, he might have been more mobile before capture in late April 1988.

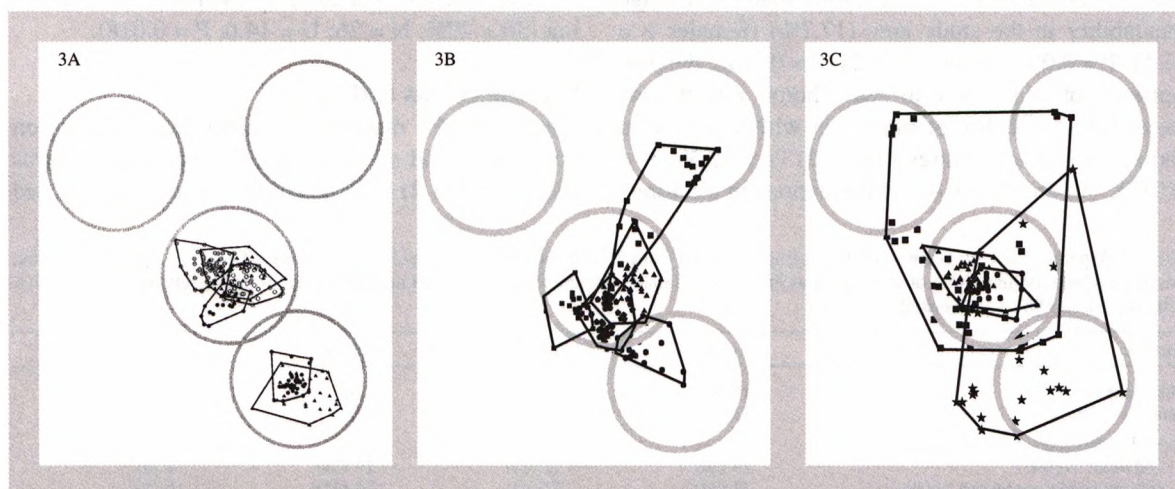Males aggregated around leks (Fig. 3) and were

Figure 3. Arrangement of the locations and home ranges of 15 radio-tagged males, 1 April - 15 May 1989: A) four old (dots) and two adult (triangles) males, B) five three-year old subadults, and C) of three two-year-old subadults and one juvenile (stars). Dotted circles indicate radii of 800 m around lek centres.

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Table 3. Distances of capercaillie locations from lek centres according to sex and age from Teisenberg, Bavarian Alps, 1988-1992. Display: 17.00-09.30; daytime: 10.00-16.30; for females, all locations were pooled; for males, the results of t-tests for differences between display and daytime locations are given.

	Distance from lek centre (m)										
	Females			Males							
				Display[1]			Daytime[2]			t-test	
Age class	x̄	SD	N	x̄	SD	N	x̄	SD	N	t	P
Juveniles				858	549	2	779	263	2		
Subadults				463	255	10	613	292	12	1.29	0.2
Adults				376	150	8	514	300	13	1.40	0.2
Older adults (pooled)	905	490	16	233	61	5	376	96	5	2.81	0.05

[1] ANOVA for age-related differences: F = 3.90, P = 0.023
[2] ANOVA for age-related differences: F = 1.42, P = 0.260

closer to the lek centre during night and main display hours than during the daytime (Table 3). Distance to the lek (see Table 3) and home range size (Table 4) were correlated (r = 0.79, N = 28, P < 0.001), decreasing with increasing age of the males, and their variation within age classes decreased from subadults to older males. Home range size was not significantly related to the proportion of old forest within the home range (r = -0.37, N = 28, P > 0.05). Site tenacity grew stronger with age; subadult males (N = 14) had used 37 ± 24% (x̄ ± SD), and adults and olders (N = 14) 71±18% of the area of their home ranges already in the previous year (t = 4.22, df = 26, P < 0.001). As an example, the spring home ranges of an individual male within a five-year period are illustrated in Figure 4.

With the exception of juveniles, capercaillie males regularly advertised their presence at dusk and dawn. During the daytime but also at night roosts and morning display sites males usually kept a distance of ≥50 m from each other; direct encounters resulted in aggressive calls, charging, or fighting. Aggression was observed not only between males of the same lek, but on two occasions during the daytime also between males of the neighbouring leks 1 and 2 at the outermost borders of their home ranges (see Fig. 3).

Nevertheless, none of the males used his home range exclusively. Particularly the home ranges of juveniles and subadults, but also those of adult and older males, may overlap those of several others (see Fig. 3). Overlap between neighbouring home ranges was related to the age of the range-holders. Display ranges overlapped less among adults or olders (N = 36, x̄ = 16%) than among subadults or between subadults and adults (N = 57, x̄ = 32%) (U = 555, P < 0.001). As indicated by the distribution of locations within the ranges, males spent most of their time in a small part of their daytime and display ranges, respectively. Including all locations, 67 and 63% of all pairs of neighbouring display (N = 18) and daytime (N = 33) ranges of adult or older males overlapped; 22 and 15% of range pairs still overlapped after the outermost 25% of the locations were excluded, but none overlapped after 50% were excluded.

Range use by females

Females stayed farther from the leks than males (U = 166, P < 0.001) (see Table 3) and their home ranges spread over an area of several kilometres around lek centres (Fig. 5). Juveniles appeared to be more mobile than adult females (Table 5). Two birds, caught in their first spring, were tracked into adult life, and

Table 4. Size [ha] of the spring home ranges (x̄, SD, N) of capercaillie males according to age class (display: 17.00-09.30; daytime: 10.00-16.30; total ranges: all locations) on Teisenberg, Bavarian Alps, 1988-92.

	Total range[1]			Display range[2]			Daytime range[3]		
Age class	x̄	SD	N	x̄	SD	N	x̄	SD	N
Juvenile	235	238	2	131	107	2	199	203	2
Subadult	105	94	10	43	32	7	75	66	10
Adult	69	43	11	16	10	6	49	32	11
Old	31	12	5	14	5	5	28	18	5

[1] ANOVA for age-related differences: F = 3.4, P = 0.033
[2] ANOVA for age-related differences: F = 6.8, P = 0.004
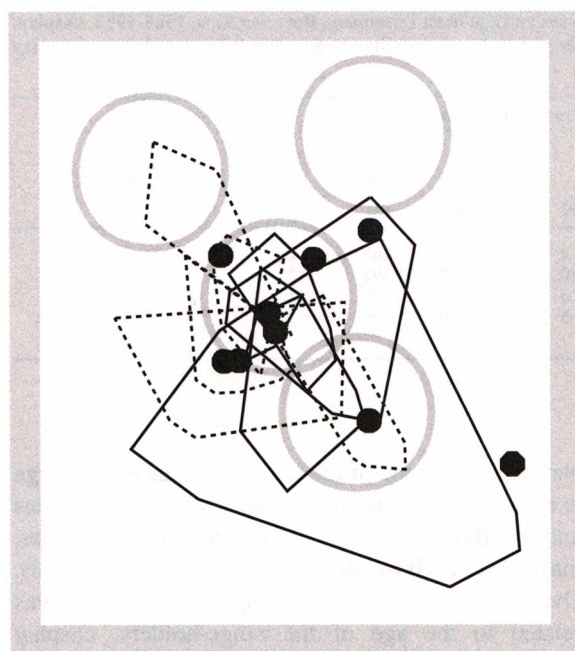[3] ANOVA for age-related differences: F = 4.0, P = 0.019

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Figure 5. Arrangement of pre-nesting spring home ranges of radio-tagged females on Teisenberg (April - May) in 1989 (solid lines) and 1991 (dashed lines). Points indicate nest locations in the following summer; circles indicate radii of 800 m around lek centres.
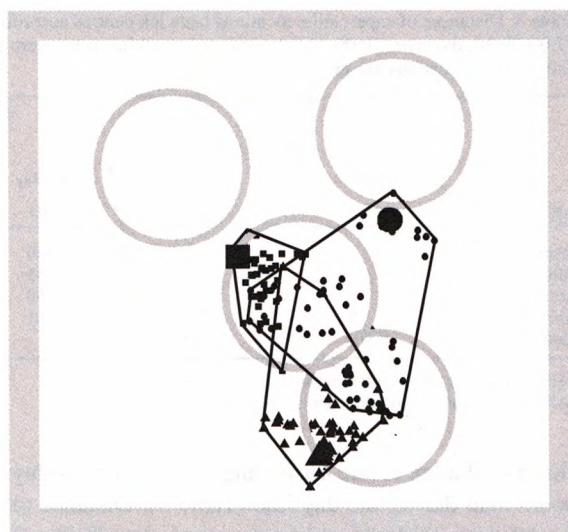

Figure 6. Examples of spring home ranges (April - May) of an adult single-lek female (squares, at left; 1991) and two adult multi-lek females (1989). Small markers indicate radio locations, large markers nest sites, and circles an 800-m radius around lek centres.

both had reduced spring home ranges as adults (843 and 165 ha as juveniles vs 262 and 119 ha as adults). They had the largest annual home ranges (April-March) (760 and 1,290 ha) of all females tracked on Teisenberg; as adults, both reduced their annual home ranges (480 and 650 ha) to about half their juvenile home range size.

Of 13 radio-tagged females four only visited the large lek 1; nine females were located at two or three leks per season, and none visited a small lek only. The number of leks visited by a hen was not related to capture on the large lek (N = 6) or off the leks (N = 7) (χ^2 = 0.03, df = 1, P = 0.78). None of five females tracked for two subsequent mating seasons changed from single-lek to multi-lek behaviour or vice versa; all visited the same leks in successive years.

The size of spring home ranges of adult females (N = 13) was related to the number of leks visited (see Table 5, Fig. 6); adult single-lek females had smaller home ranges than adult multi-lek females (t = 3.86, P < 0.01). Home range size of single-lek females (r = -0.81, P = 0.03) but not multi-lek females (r = -0.41, P = 0.27) decreased with increasing proportions of preferred habitat, i.e. old forest, within their home ranges. Although single-lek females had greater proportions of old forest in their home ranges (46.2 ± 24.6% ($\bar{x}$ ± SD) vs 24.7 ± 5.0%; t = 2.26, df = 11, P = 0.05), the total old forest area available was greater in the home ranges of multi-lek females (22.5 ± 10.5 ha vs 45.0 ± 20.9 ha; t = 2.38, df = 11, P < 0.05). Home range diameter was smaller than inter-lek distance (1.9 ± 0.5 km) in adult single-lek females (t = 2.34, df = 8, P < 0.05) but not in adult

Table 5. Size and diameter of spring home ranges of capercaillie females, according to age class and number of leks visited, Teisenberg, Bavarian Alps, 1988-1992.

Age class/leks visited	N	Home range size (ha)[1]			Home range diameter (km)[2]		
		Range	$\bar{x}$	SD	Range	$\bar{x}$	SD
Juveniles	3	68 - 843	359	422	1.2 - 4.2	2.4	1.6
Adults	14	17 - 278	137	92	0.9 - 6.9	2.2	1.5
Adult single-lek females	6	17 - 96	60	30	0.9 - 1.7	1.3	0.3
Adult multi-lek females	7	93 - 278	186	80	1.7 - 2.9	2.4	0.4

[1] single vs multi-lek females: t = 3.86, df = 11, P < 0.01
[2] single vs multi-lek females: t = 5.65, df = 11, P < 0.001

multi-lek females (t = 1.44, df = 9, not significant). Some multi-lek females mainly used part of their home range near one lek, visiting other leks only during repeated excursions of 2-3 days (see Fig. 6, southern home range), whereas others used their home ranges more evenly (see Fig. 6, eastern home range).

There was no difference in the size of winter home ranges between adult single and multi-lek females (126 ± 105 ha, N = 4 vs 169 ± 143 ha, N = 5, U = 7.0, P = 0.56). However, adult multi-lek females had larger summer home ranges (166 ± 84 ha, N = 8 vs 92 ± 20 ha; N = 4, U = 4.0, P = 0.04) and annual home ranges (565 ± 115 ha, N = 4 vs 218 ± 120 ha, N = 4, W = 10.0, P = 0.02) than adult single-lek females. In summer and in winter, multi-lek females were farther from the large lek than single-lek females (summer: $\bar{x}$ ± SD = 1,377 ± 759 m vs 690 ± 175 m, t = 2.43, df = 10, P < 0.05; winter: 1,777 ± 775 m vs 820 ± 365 m, t = 2.75, df = 7, P < 0.05).

Nest sites (N = 13) of both radio-marked single and multi-lek females (U = 11.0, P = 0.40) were at distances of 0.2 - 6.2 km from the lek the hen most frequently attended (1.3 ± 1.7 km ($\bar{x}$ ± SD), median 0.7 km). One adult hen nested outside the study area on the neighbouring mountain; nearest-lek distances of nest sites in the study area ($\bar{x}$ ± SD = 0.8 ± 0.5 km, N = 12) were normally distributed (K-S Z = 0.78, P = 0.57) and were not different from nearest-lek distances of random points (U = 74.0, P = 0.827).

Discussion

Habitat selection

Resource distribution is considered a major determinant of the variation observed among grouse mating systems (e.g. Wiley 1974, Wittenberger 1978, Bradbury 1981, Payne 1984, Bergerud 1988). Reports on ruffed grouse (Gullion 1976) and blue grouse (Lewis 1985) indicate that clustered male territories may result from attraction to a particular resource, such as patches of feeding trees. As elsewhere (Seiskari 1962, Hjorth 1982, Rolstad & Wegge 1987a), capercaillie on Teisenberg preferred old forest throughout the year (Storch 1993a, 1993b, 1994, this study). Old forest was patchily distributed within a mosaic of younger successional stages. Thus, it is relevant to ask if the distribution of old forest explains aggregation of males? For the capercaillie population studied, there was no such evidence; patches of the preferred habitat type, old forest, were available throughout the

area. In spring, males and females both preferred old forest (this study) and fed on the same food plants (Storch et al. 1991) but only male home ranges were clustered. Furthermore, males preferred old forest throughout the year but aggregated only in spring (Storch 1993a,b, 1995).

Lek centres were in old forest, but their surroundings were highly fragmented. This was reflected by more display than daytime locations of males in old forest. Preliminary results from this study agreed with findings from the boreal forest, which indicate that the number of males per lek may be associated with availability of old forest (Wegge & Rolstad 1986, Rolstad & Wegge 1989) and that habitat fragmentation may increase predation risk (Gjerde & Wegge 1989). Thus, it is likely that in the Alps forestry practices also influence dispersion and dynamics of capercaillie populations.

Spacing of leks and males

Interlek-distances reported from various parts of the range vary around 2 km (Wegge & Rolstad 1986, Catusse 1988, Beshkarev, Blagovidov, Teplov & Hjeljord 1995, R. Moss, pers. comm.). A recent survey from the central Alps (Keler 1991) confirmed this pattern, as did my study. In Norway (Wegge & Rolstad 1986) and on Teisenberg, most male locations were within a radius of half the interlek-distance from lek centres, indicating that the spacing of leks may result from the spatial requirements of males (Wegge & Rolstad 1986).

Hjorth (1982) first described the spatial organisation of capercaillie leks as a piece-of-pie pattern with largely exclusive individual home ranges extending radially from the lek centre. Wegge & Larsen (1987) argued that the spacing pattern of male capercaillie resembles that on true leks rather than the dispersed territories found in North American forest grouse, however, in contrast to typical lekking species, which are territorial only at the display site, capercaillie males seem to establish permanent spring territories which include daytime ranges. My results, which report the first data on the spatial organisation of capercaillie leks in Central Europe, are in general agreement with the patterns observed in Scandinavia.

A territory is defined as an area exclusively used by an individual in time or space, and results from avoidance of or overt aggression towards conspecifics (Davies 1978). Mutual avoidance and stable spatial arrangement confirmed that the spring home ranges of male capercaillie may be considered territories

(Wegge & Larsen 1987). When flushed during daytime on Teisenberg, males were always alone (N = 75) and, with the exception of juveniles, were aggressive towards each other. Still, there was substantial overlap among individual home ranges. However, probably by advertising and aggressive behaviour, males were well separated in time, even when their home ranges completely overlapped in space.

Juveniles and some subadults are non-territorial, as they explore several leks and use large, poorly defined home ranges, which overlap the home ranges of several other males (Wegge & Larsen 1987, this study). New recruits to a lek may settle in unclaimed areas between the territories of older birds, as described by Wegge & Larsen (1987). At large leks such as lek 1 on Teisenberg, where there are hardly any unclaimed areas left, young males may completely share an older male's territory, however. Territorial traits grew stronger with age; home ranges became smaller, overlap with neighbouring home ranges decreased, while site tenacity increased (Gjerde, Wegge, Pedersen & Solberg 1985, Wegge & Larsen 1987, Catusse 1992, this study) with adult and old males using the central parts of their home ranges exclusively. In contrast to other seasons (Storch 1993a,b), the variation in male spring home range size could not be explained in terms of habitat composition.

In capercaillie males, social dominance is age related (Wegge & Larsen 1987, Catusse 1992). Reproductive success is skewed, as most females seem to choose the same, dominant male for mating (Hjorth 1970, Wegge & Larsen 1987). Thus, old males primarily compete with each other for social rank and consequently for matings, and therefore may tolerate younger birds within their territories, whose mating chances may be poor even though they show full display behaviour. Little may be gained from expelling subordinates, whereas costs may be high. Once a male settled at a lek, he would remain in his home range; young males, however, moved closer to the lek centre with consecutive years, while older males attempted to hold their territories. Although highest at the lek centre, dominance is not bound to any particular position (Wegge & Larsen 1987). Therefore, lek centres may shift between years, as the social status of individuals changes. A young male that shares the territory of an old high-ranking male may eventually replace him. Thus, the description of young males as standby rather than surplus birds (Wegge & Larsen 1987) appears appropriate.

To summarise my results and those of others (Hjorth 1982, Wegge & Larsen 1987), adult and some subadult capercaillie males use confined territories at a lek and are aggressive towards each other; at least at small leks, their territories are largely exclusive (Hjorth 1982, Wegge & Larsen 1987). At large leks, however, they may not fully monopolise a range and territories may greatly overlap in space, although the birds are still well separated in time. In conclusion, the classical piece-of-pie model with exclusive territories extending radially from the lek centre (Hjorth 1982) applies only for leks with a restricted number of males. For larger leks such as on Teisenberg, the pie of the model has to be multi-layered.

Range use by females

Numerous theories have been advanced to explain evolution and spacing of leks (see Höglund & Alatalo (1995) for a review). Bradbury (1981) and Bradbury & Gibson (1983) developed two alternative lines of thinking: according to the 'hotspot' model, males cluster in locations preferably used by females. In the 'female-preference' model, leks result from female preference for aggregations of males. Both models are based on the size of female home ranges in relation to spacing of leks; in the hotspot model, leks will be more closely spaced than the diameter of female home ranges, and females visit several leks. In the female preference model, leks are at least one female home range diameter apart and most females visit only one lek (Bradbury 1981, Bradbury & Gibson 1983, Bradbury er al. 1986).

Field studies on greater prairie-chickens *Tympanuchus cupido* (Schroeder 1991), sage grouse *Centrocercus urophasianus* (Bradbury, Vehrencamp & Gibson 1989a, Bradbury, Gibson McCarthy & Vehrencamp 1989b), and great snipe *Gallinago media* (Höglund & Robertson 1990) all reported that a majority of females visited several leks and rejected the female preference model. Evidence from capercaillie is ambiguous. Whereas Norwegian data on female home ranges were inconsistent with the predictions of both models (Wegge & Rolstad 1986), findings from the Pyrenees were in accordance with the hotspot model and suggested that a patchy distribution of nesting habitats led to aggregations of females, which determined the spacing of leks (Ménoni 1991).

In agreement with the Norwegian study (Wegge & Rolstad 1986) both hypotheses have to be rejected for the Teisenberg population. In contrast to the predic-

tions of the female-preference model, two thirds of the females on Teisenberg visited several leks and used spring home ranges wider than interlek-distance. In contrast to the hotspot model, one third of the females visited one lek only and had home ranges smaller than interlek-distance. Also, as described for other species such as sage grouse (Wakkinen, Reese & Connelly 1992), winter home ranges (Gjerde & Wegge 1989, Storch 1995) and nest sites (Wegge 1985, Storaas & Wegge 1987, this study) of capercaillie females were spaced independently of leks.

Movements by females of lekking species may be influenced by factors such as climate, food, cover, predation, dispersion of males, and behavioural differences among age-classes and individuals. Therefore, the great variability in female home range size documented for the Teisenberg population should not be surprising. Preliminary data from this study indicate that female capercaillie explore their surroundings during their first year of life, whereas adult range use patterns seem to be largely fixed; site fidelity is strong in capercaillie (Wegge 1985, Klaus, Andreev, Bergmann, Müller, Porkert & Wiesner 1989, Storch 1995) and other grouse (Bergerud & Gratson 1988), and the birds return to the same seasonal home ranges, leks, and nesting areas year after year.

The only published data on lek visitation by female capercaillie are from Norway, where most females visited only one lek and used some 50 ha spring home ranges (Wegge & Rolstad 1986), as did single-lek females from Teisenberg. Multi-lek females used home ranges several times that size. In contrast to other seasons, when female home range size was negatively related to habitat quality (Storch 1993a,b, 1995), enlarged home ranges of multi-lek females did not result from poor availability of preferred old forest habitat and thus have to be explained in other terms.

As females of other lekking birds (Gibson & Bradbury 1986, Pruett-Jones & Pruett-Jones 1990, Trail & Adams 1989, Gibson & Bachmann 1992), capercaillie females apparently actively assessed several potential mates. They may make their mate choice from a large number of males, as indicated by the observation that all radio-tagged Teisenberg females visited the large lek and none visited a small lek only. Lek size is related to habitat features; Norwegian studies showed that the number of males per capercaillie lek decreases with old forest fragmentation (Rolstad & Wegge 1987b). Where leks are small, females have to travel longer distances in order to assess an equal number of males, which may be costly in terms of increased energy expenditure and predation risk. Hence, females may compromise between costs and benefits of sampling potential mates. Where leks get smaller, and if costs are small, as was shown for sage grouse (Gibson & Bachman 1992), they may eventually shift from single-lek to multi-lek behaviour, i.e., female range use would be a function of male dispersion.

In the boreal forest, the capercaillie's main distribution range, leks with several adult males are regularly spaced (Wegge & Rolstad 1986, Beshkarev et al. 1995) and females generally visit one lek (Wegge & Rolstad 1986), whereas only one such lek was available on Teisenberg. As their summer and winter home ranges were farther from the large lek than those of single-lek females, enlarged spring home ranges of multi-lek females may result from the dispersion of males. Furthermore, individual differences in mobility may be involved as multi-lek females also had larger summer and annual home ranges than single-lek females.

Based on computer simulations Gibson, Taylor & Jefferson (1990) concluded that in lekking species a wide range of spacing patterns may result depending on the relative weight of influencing factors. The studies of capercaillie support this notion. In comparison with Scandinavian results (Wegge 1985, Wegge & Rolstad 1986), the findings from Teisenberg suggest that females may be far more flexible in range use and lek visitation than generally assumed in models of lek evolution. The great intraspecific variability in female movements indicates that observations of female home range size in relation to lek spacing are unsuitable to provide critical tests of lek evolution hypotheses in capercaillie.

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