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Spring spacing behaviour of capercaillie *Tetrao urogallus* males does not limit numbers at leks

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Studies in Fennoscandia and Central Europe have shown that in spring male capercaillie establish more or less exclusive home ranges around leks. Thus, such territorial spacing behaviour might limit the number of males at leks. However, the results of our study in the Pinega Reserve, a pristine boreal forest in northwestern Russia, during the springs of 2000 and 2001 do not support this hypothesis. Home ranges of radio-collared birds (N = 11) at a lek with > 25 attending males were almost completely overlapping. The ranges of adults were of the same general size (47.5 ha) and were distributed within the same distance (ca 1 km) from the lek centre as reported elsewhere. Also, as found in other studies, yearlings and two-year olds did not have well-defined ranges; yearlings visited other leks and adults returned to the same lek and daytime ranges in successive years. The inter-lek distance between the three large leks was longer (4.0 km) than reported from smaller leks in two study areas in Norway (2.0 and 2.1 km). However, the inter-lek zone beyond the two 1 km radii of adjacent leks appeared not to be occupied by adult males attending these leks. In spite of largely overlapping ranges, adults tended to avoid each other. The mean distance between eight of 10 possible pair combinations of five males located simultaneously within their combined ranges were significantly farther apart (P < 0.05) than random pair distances. Thus, a system of hierarchical dominance may act to adjust the day-to-day positions of neighbours, but it has little effect on the number of males attending a lek.

Key words: capercaille, grouse, lek, spacing behavior, Tetrao urogallus, Russia

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The capercaillie *Tetrao urogallus* has a clumped, polygynous, lek type mating system (Wiley 1974, Oring 1982, Wegge & Larsen 1987). The 5-25 ha display grounds (Pirkola & Koivisto 1970, Hjorth 1970) are confined to the later seral stages of the boreal forest (Rolstad & Wegge 1987), and in continuous, optimum habitat they are regularly spaced with an inter-lek distance of ca 2 km (Wegge & Rolstad 1986). Although males attend the leks from early April to the end of May, females only visit the leks for a few days for mating. Copulation success of males is skewed, as most females choose the same dominant male for mating (Hjorth 1970, Wegge & Larsen 1987, Höglund & Alatalo 1995).

Hjorth (1982) has suggested that the spatial distribution of male capercaillie resembles a piece-of-pie pattern, with largely exclusive individual daytime home ranges radiating from the morning display sites at the lek. Telemetry studies in Norway (Larsen, Wegge & Storaas 1982, Wegge & Larsen 1987) and Germany (Storch 1997) confirmed that this pattern was true for adult males > two years of age during the breeding season, and that yearlings and many two-year old males were non-territorial and moved among leks. Whereas the young birds may visit several leks during a season, older males return to the same lek and daytime territories (*sensu* Davies 1978) during successive years. Daytime territories furthest away from the lek centre tend to be larger and occupied by younger adults than those close to the lek centre, and the maximal distance from the centre was ca 1 km (Wegge & Larsen 1987, Storch 1997).

Wegge & Rolstad (1986) showed that the size of daytime territories was inversely related to the proportion of optimum habitat within them, i.e. with continuous old natural forest the size of the territory decreased to 15-20 ha. From the observed spacing relationships, Wegge, Rolstad & Gjerde (1992) inferred that the spacing behaviour of males outside the display ground not only regulate inter-lek distance, but also may limit the number of males at leks. Hence, if truly territorially distributed, the maximal number (of adult males > 2 years of age) in optimum habitats should be < 20 resident males.

The studies referred to above were all conducted at small and medium-sized leks in forests modified by human activities. Popular literature has reported leks with 30 or more attending males, and one of the leks studied by Storch (1997) numbered 15-20 males. Storch (1997) showed substantial total range overlap among males at this lek and suggested that on such large leks 'the pie of the model has to be multi-layered'. The question has therefore arisen whether the conceptual framework of territoriality is maintained at large leks, and hence, whether male territorial behaviour puts an upper limit to the number of resident males at leks.

Our study reports on the spacing relationships of males at large leks in a pristine boreal taiga forest in northwestern Russia. We assessed two alternative hypotheses: 1) for territoriality to be functioning at very large leks, the daytime territories must either be much smaller than reported from Fennoscandia and western Europe, or the inter-lek distance must be larger to allow for more birds to settle, and 2) true territorial spacing is not maintained at very large leks.

Methods

Study area

Our study was conducted during the springs of 2000 and 2001 in the 421 km^2 Pinega Reserve (State Natural Reserve Pinezhskiy; 64° 35' N, 42° 80' E) in northwestern Russia, ca 400 km east-northeast of Archangelsk. The climate is continental with a mean temperature of 14.3°C in July and -14.7°C in January. Generally, snow covers the ground from late October to mid May. The terrain is flat with a high ground water table which gives rise to boggy ground conditions during the spring snow melt.

The dominant vegetation type is old-growth *Vaccinium*-spruce *Picea obovata* x *abies* forest intermixed with Scots pine *Pinus sylvestris* and larch *Larix sibirica*. Birch *Betula* spp. and aspen *Populus tremula* are the most common deciduous tree species, and bilberry *Vaccinium myrtillus* and bog bilberry *V. uliginosum* dominate the ground layer. The eastern part contains secondary mixed forests originating from forest fires before 1960 (21% of the reserve) and logging during 1960-1970 (7% of the reserve). About 10% is covered by open peat bogs of which the largest proportion is located in the southwestern part.

Like in all Russian 'zapovedniki' (strictly protected reserves), human activity inside the reserve is minimal. The wild fauna is typical of undisturbed, northern boreal forests with relatively low numbers of large carnivores and moose *Alces alces*. The main predators of forest grouse are goshawk *Accipiter gentilis*, common buzzard *Buteo buteo* and pine marten *Martes martes*. Red fox *Vulpes vulpes* is very rare, but more common outside the reserve closer to human settlements. Four species of grouse are found in the reserve: willow ptarmigan *Lagopus lagopus* and black grouse *Tetrao tetrix* are mainly found near the open peat bogs, whereas hazel grouse *Bonasa bonasia* and capercaillie are distributed throughout the whole reserve. The density of hazel grouse is high in August (> 50/km^2), whereas capercaillie occur in moderately high densities (ca 5/km^2; Borchtchevski, Hjeljord, Wegge & Sivkov 2003).

Telemetry

During the breeding seasons of 1999-2001, 55 males were captured in ground nets at three neighbouring leks in the central part of the reserve. Among the males ≥ two years of age, sampling was assumed to be random; only yearlings are expected to be under-represented when using this capture method (P. Wegge, unpubl. data). Each male was equipped with a 35-g necklace type transmitter in the 142-143 MHz frequency range, and morphometric data, including beak measurements, were recorded. Males were classified according to age based on beak depth measurements according to the description by Moss, Weir & Jones (1979), as modified by Wegge & Larsen (1987). Yearlings included males with beak depths < 23.0 mm, assumed to be 10-11 months old, two-year-olds included males with beak depths of 23.0-25.5 mm, assumed to be 22-23 months of age, and adults included males with beak depths > 25.5 mm, assumed to be ≥ three years old.

Two of the leks were attended by > 25 males and the third lek by an estimated 12-14 males. The average distance between leks was 4.0 km. One of the two largest leks was selected for intensive monitoring of male spacing behaviour. At this lek, six males were collared in 1999, 14 in 2000 and four in 2001. Due to losses to predators and depletion of transmitter batteries, the total number monitored at this lek was 11 in 2000 and five in 2001; three of the birds were monitored both years.

Most daytime locations were determined by triangulation; we plotted the compass bearings from three or more elevated terrain points using a portable receiver and a directional hand-held 4-element Yagi antenna. Each male was located between 10:00 and 17:00 hours once or twice a day, seven days a week. Tracking intensity and precision of radio-locations varied between the two spring seasons. Hence, the data sets were split in two: in 2000, the 11 males were located a total of 101 times, of which 29 were from crossbearings and the rest from triangulations with a mean precision of ca 1.0 ha/location. Thus, the data in 2000 gave rather imprecise locations which tended to overestimate space use and distance from the lek. In 2001, the five males were located 124 times with a mean precision of 0.15 ha/location. Because of the less frequent and imprecise locations in 2000, the data set collected that year was used mainly to illustrate the extent of range overlaps, age variations and general movements. The data from the intensive tracking of the fewer birds in 2001 were used for estimations of home range size, quantification of range overlaps, distribution occupancy centres and analysis of spatio-temporal relationships.

The period of data collection lasted for 27 days in 2000 and 33 days in 2001, each year covering the mating period of about one week and 3-3.5 weeks thereafter (until the males abandoned the lek and migrated to their summer ranges). The sample of 11 birds in 2000 represented 35-40% of all males attending the lek that year, whereas the small sample of five males in 2001 represented a much smaller proportion. Hence, in both years many unmarked males were also present at their daytime ranges that intermingled with the ones we monitored using telemetry.

In general, the estimated home range size increases with number of locations until an asymptotic relationship is attained. For adult male capercaillie spring home ranges in Norway, > 90% of the total home range size was reached at ca 20 locations (Wegge & Larsen 1987). All males in 2001 were located a minimum of 20 times, and to minimise autocorrelation, consecutive locations were separated by more than six hours.

Data analysis

To be able to compare the home range data with those obtained in an earlier study in Norway, we estimated home range size by use of Harvey & Barbour's (1965) "Minimum Area Method", as modified by Wegge & Larsen (1987). Polygons were drawn among successive outermost points that were spaced less than half the distance between the two most widely separated locations. This method produces a range size estimate roughly 10-15% smaller than the size estimate calcu-

Table 1. Morphometric data including date of capture, beak depth (in mm), body mass (in kg), age (in years) and number of locations, daytime range sizes (in ha) and daytime range overlap (in %) of capercaillie males (numbered by the frequency of their transmitters) at a large lek (> 25 males) in the Pinega Forest Reserve, Russia, during the springs of 2000 and 2001.

Male no.	Date of capture	Beak depth	Body mass	Age	No. of locations 2000	No. of locations 2001	Range size 2000[a]	Range size 2001	Range overlap 2000	Range overlap 2001
125	08.05.99	25.3	4.1	~ 2[b]	9	-	30.9	-	100	-
257	29.04.00	26.5	4.8	> 2	10	25	36.6	38.4	63.3	87.0
327	29.04.00	26.2	4.5	> 2	11	-	90.2	-	77.6	-
376	29.04.00	25.9	4.7	> 2	10	-	152.3	-	67.2	-
287	29.04.00	25.8	4.5	> 2	10	22	100.8	58.3	74.4	93.7
396	29.04.00	27.0	4.4	> 2	11	20	16.3	40.7	94.7	81.8
246	30.04.00	27.4	4.4	> 2	10	-	13.7	-	90.9	-
367	30.04.00	25.5	4.5	~ 2	9	-	62.8	-	75.2	-
057	08.05.00	20.5	3.6	< 1	9	-	4.8	-	100	-
085	10.05.00	25.2	4.4	~ 2	5	-	6.8	-	100	-
302	10.05.00	26.0	4.5	> 2	7	-	33.2	-	58.5	-
685	05.01.01	26.5	4.4	> 2	-	22	-	62.8	-	82.8
855	07.05.01	26.9	4.6	> 2	-	35	-	37.3	-	100
Means							(49.9)	47.5	82.0	89.1

[a] Range size based on few and imprecise locations (see text)
[b] Bird was three years old when monitored in 2000

lated by use of the Minimum Convex Polygon (MCP) method (Eliassen 2000).

The range overlap of each bird was measured as the proportion of its range that was overlapped by the combined ranges of all the other radio-collared males.

To determine whether males were avoiding each other or not, we compared the distances between males which were located at the same time with the distances between two random locations within their combined daytime ranges. We did this for all 'pairs of males' (N = 10) that were triangulated simultaneously in a total of 81 times. If the average distance between the pairs of males was significantly longer than the average distance between pairs of random locations within their combined ranges, the birds were more dispersed than random.

The geographical centre of each male's daytime locations, termed "Occupancy Center" (Wegge & Larsen 1987), was calculated as the mean of the distribution of radio locations along the y and x-coordinates, and its distance from the lek centre was measured by use of GIS. Similarly, the maximum distance moved by each bird from the lek centre was derived from GIS analysis.

All telemetry locations were transferred to UTM coordinates, digitalized and analysed using ArcView 3.2 and Map Source 3.02.

Results

Range size and distance from lek

All five radio-tagged males in 2001 were estimated to be at least three years old. Their daytime range sizes varied from 37.3 to 62.8 ha, averaging 47.5 ha (Table 1). There was no relationship between daytime range size and bird mass ($P > 0.41$) nor beak depth ($P > 0.27$), possibly due to little variation in body mass and age among the sampled birds. Most occupancy centres were located 300-600 m from the lek, and only 6.7% of all daytime locations were further away than one km from the lek (Table 2).

Table 2. Daytime distribution expressed by distance from the lek (in m) of 16 radio-tracked capercaillie males around a lek with > 25 attending males in the Pinega Forest Reserve, Russia, during the springs of 2000 and 2001.

	Occupancy centre		Locations	
Distance from lek (m)	Number	%	Number	%
0-250	0	0	14	6.2
250-500	8	50.0	84	37.3
500-750	7	43.7	87	38.7
750-1000	1	6.3	25	11.1
≥ 1000	0	0	15	6.7
Total	16	100	225	100

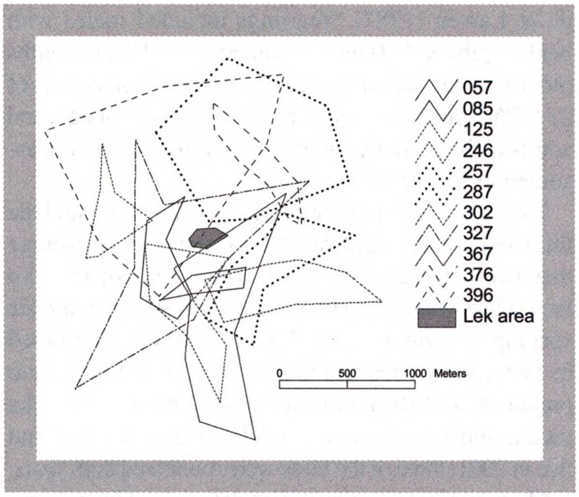

Figure 1. Distribution of daytime ranges of 11 males at a lek with > 25 attending males in the Pinega Forest Reserve, Russia, during spring 2000.

Movement and site fidelity

In 2000, the data included a few young birds. Due to a less precise and insufficient number of locations, their range sizes could not be compared directly. However, from daily tracking, both a yearling (# 057) and one of the two-year old males (# 085) were suspected to have visited other lek(s), and a yearling at another lek was known to have done so. None of the older males was known to have visited more than one lek during the same season. Three adult males that were monitored in both years (# 257, 287 and 396) used roughly the same ranges in successive years. During daytime, the males did not use certain areas within their ranges more intensively than others, as there was no tendency for clumping of locations within any of the ranges.

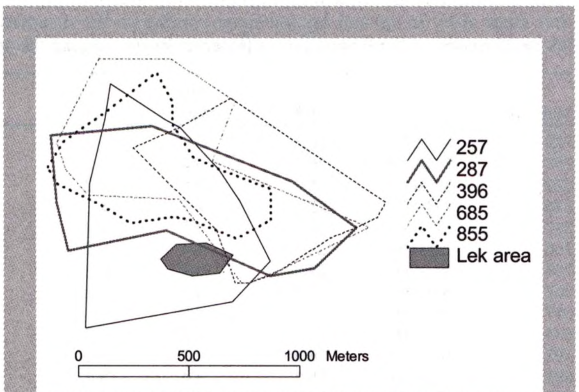

Figure 2. Distribution of daytime ranges of five adult males at a lek with > 25 attending in the Pinega Forest Reserve, Russia, during spring 2001.

Table 3. Mean distances (in km) between pairs of adult males located simultaneously and random pair locations within their combined daytime ranges in 2001. About 80% of the paired distances occurred when both birds were in the zone of overlap (see text).

Pair of males	Mean distance		Two sample t-test	
(bird frequencies)	Observations	Random	t-value	P-value
257 - 287	0.52	0.26	2.11	0.032*
257 - 855	0.48	0.22	2.06	0.039*
257 - 396	0.76	0.41	2.87	0.008**
257 - 685	0.53	0.41	0.97	0.194
287 - 855	0.44	0.23	2.19	0.027*
287 - 396	0.80	0.39	3.10	0.005**
287 - 685	0.66	0.45	2.37	0.025*
855 - 396	0.84	0.43	3.04	0.004**
855 - 685	0.27	0.16	1.56	0.089
396 - 685	0.72	0.47	3.52	0.008**

* Significant difference at 95% probability level (one-tailed)
** Significant difference at 99% probability level (one-tailed)

Spatio-temporal relationships

The daytime ranges almost completely overlapped in both 2000 and 2001 (Figs.1 and 2). In 2000, the mean extent of overlap for 11 males was 82.0%. In 2001, the much smaller sample of five birds, representing only about 1/5 of the total number of males attending the lek, overlapped by 89.1% (see Table 1). Thus, daytime ranges were clearly not separated spatially. However, when located at the same time, eight of 10 paired males were significantly further apart from each other than if randomly distributed within their combined daytime ranges ($P < 0.05$; Table 3).

Discussion

During daytime, in the breeding season, capercaillie males may be distributed in three different patterns at large leks: 1) in largely exclusive and small territories within a restricted area surrounding the diplay ground (henceforth lek area), 2) in territories distributed over a larger total lek area, or 3) in overlapping, non-territorial home ranges. At the large leks we studied in Russia, males were clearly distributed in a non-territorial pattern, unlike the pattern described from smaller leks in Norway (Wegge & Larsen 1987) and Germany (Storch 1997). Daytime home ranges overlapped by > 80%, but individual ranges were of the same size as reported in the earlier studies. The total lek area was also of similar size, as males were confined within a radius of 1 km of the centre of the lek. The spacing pattern was similar to what Storch (1997) reported from a large lek in the German Alps. Thus, we reject the hypothesis that the number of capercaillie males at leks may be limited by territorial spacing behaviour (Wegge et al. 1992).

In spite of the largely overlapping ranges, the males at the large leks in the Pinega Reserve seemed to avoid each other during daytime. Thus, by reducing visual contact, confrontations and energy-draining agonistic behaviour are presumably minimised (Wegge & Larsen 1987). At Varaldskogen in Norway, Eliassen (2000) found that during daytime, subdominant adult males more often withdrew from the overlapping zone than higher-ranking males, and that playback experiments triggered overt aggression among some individuals outside the lekking ground. Thus, a dominance hierarchy (*sensu* Maher & Lott 1995), as was suggested within daytime ranges by Eliassen (2000), may space out neighbours temporally. However, such avoidance behaviour mainly adjusts the mutual positions temporally and has little limiting effect on number of birds settling at the lek.

The average inter-lek distance between the three large study leks in the Pinega Reserve was ca 4 km, and all 23 leks within the reserve were regularly spaced with a mean minimum inter-lek distance of 2.5 km (Andreassen 2001). In Norway, the mean inter-lek distances between >13 leks in two study areas were 2.0 and 2.1 km, respectively, corresponding to twice the maximum distance moved by individual males from their lek centres during daytime (Wegge & Rolstad 1986). From this and the non-random, regular distribution of leks, Wegge & Rolstad (1986) inferred that lek spacing in capercaillie is related to the spacing behaviour of males and not to that of females, as suggested by the models proposed by Bradbury & Gibson (1983). The larger distance between the leks in the Pinega Reserve may therefore explain their larger numbers of males; more space is available between the leks for birds to settle. However, at the large lek studied, adult males did not occupy space beyond 1 km of the lek. Neither did we observe males to move further away from the leks at the other two leks we studied, in spite of suitable habitat. Seemingly, an inter-lek zone between the 1 km radii of neighbouring leks was not occupied by lek-attending males during the breeding season.

With increasing loss of suitable habitat around the leks caused by clearcutting of forests in Norway, the number of males at traditional leks has decreased, but new, small leks are being established in patches of medium-aged cultivated forests and remnant old-forest patches (Rolstad & Wegge 1989b, Gjerde, Rolstad, Wegge & Larsen 1990). Lek dynamics in capercaillie therefore poses a puzzling question: if males do not distribute themselves territorially as now documented at larger leks, why do they establish separate leks at 2-4 km distance throughout the forested landscape? The answer is probably that in lekking species, breeding males are recruited from the outside, i.e. from the peripheral part of the lek area (Wiley 1974), and that male mating success is related to bird age. At very large leks, the probability of a young male mating successfully in its lifetime is reduced below a certain treshold level, so he will prefer to settle at another lek with fewer males. This may be the situation in large, continuous forests, like in the Pinega Reserve in Russia. But why are new leks established when the number of males at existing leks is quite low, as seen in the fragmented forests in Norway? A likely explanation is that reduced habitat quality around established leks due to forestry operations in some way provides cues for younger males to attempt to form new leks elsewhere, such as in areas occupied by females in late winter (Gjerde, Wegge & Rolstad 2000), or in areas with high nest densities (Menoni 1997). However, new leks are also formed when vacant space of suitable male habitat quality is available at already established leks (Rolstad & Wegge 1989a, Wegge & Rolstad, unpubl. data). Hence, space and habitat limitations are not the only factors that trigger formation of new leks in boreal forests.

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