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# On the spatial relationship of males on "exploded" leks: the case of Capercaillie grouse *Tetrao urogallus* examined by GPS satellite telemetry

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The mating system of Capercaillie has been referred to as "exploded lek" because displaying males are spaced farther apart than on classical leks. However, inter-male distances and spacing behavior rarely have been quantified. In 2009–2011, we examined the spatial relationships of males on two leks in southeastern Norway by GPS satellite telemetry. Largely exclusive display territories (median 2 ha) surrounded the mating site, but the males spent most of the time displaying on smaller, well-defined display sites (median 182 $m^2$) within their territories. When on their display sites, neighboring birds were spaced 64–212 m apart; decreasing to a minimum during the time of mating. Occasionally, males made long exploratory excursions (median 243 m) across the territories of neighbors, sometimes interacting with them at close distance (< 10m). During daytime, males resided solitarily in radially extending ranges within 1 km of the lek center, commuting to the lek either in the evening or morning by walking or flying, leaving in the morning mostly by walking. The distance from the lek center to night roosting trees and daytime resting areas decreased during the mating season. With interacting males and a spatial arrangement in-between that of classical leks and dispersed polygyny, the term "exploded lek" seems appropriate for the mating system of Capercaillie.

## 1. Introduction

The mating system of polygynous grouse forms a continuum from males displaying solitarily in dispersed territories to males being highly aggregated at communal arenas referred to as leks (Wiley 1974). "Classical" leks are mainly found among steppe and prairie-dwelling species, while territorial clumping is far less pronounced among forest-dwelling species (Wittenberger 1978, Bergerud 1988). The mating system of the large, forest-dwelling Capercaillie *Tetrao urogallus* has been difficult to define along this gradient. More than 50 years ago, Lumsden (1961) reported that in this species males were spaced farther apart than on true leks, and Hjorth (1970), in his description of the reproductive behavior of grouse, referred to its mating system as "lek-like". More recently, in their comprehensive review of leks, Höglund & Alatalo (1995) classified the mating system of Capercaillie as "exploded" lek, a term first coined by Gilliard (1963) for more loosely clumped poly-

Table 1. Explanation of the terms used to describe the lek system of the Capercaillie, as outlined in Fig. 1.

| Term | Definitions |
|---|---|
| *Lek area* | Consists of the mating site, the display territories with display sites, and the innermost portions of the daytime area of the males attending the lek. (Only males of age ≥ 2 years establish display territories and daytime ranges – juveniles are non-territorial without fixed ranges (Wegge & Larsen 1987)) |
| *Lek center* | The geographical center of the attending, displaying males |
| *Mating center* | Location where all – or the majority of – matings take place |
| *Display territory* | Largely exclusive area on the lek where the male performs display |
| *Display site* | Smaller area(s) within the display territory where the male performs most of the display activities |
| *Daytime range* | An area extending radially up to 1 km out from a male's display territory on the lek, wherein the male resides during the day when not engaged in lekking activity |
| *Daytime core area* | An area within the daytime range where males exhibit territorial behavior (Wegge *et al*. 2005) |
| *Daytime ground resting site* | Location within the daytime area where the male resides during daytime (*sensu* Finne *et al*. 2000) |
| *Daytime occupancy center* | Mean geographical location of all daytime locations relative to the center of the lek (*sensu* Wegge & Larsen 1987) |
| *Night roosting tree* | Tree in which the bird roosts during the night, located either in the display territory on the lek or in the daytime area close to the display territory |
| *Excursion* | Directional male movement from own display territory into or across neighboring male's territory |

gynous species. On a landscape scale, where Capercaillie leks are regularly spaced at 2–3 km distance (Wegge & Rolstad 1986, Rolstad *et al.* 2009), displaying males are still highly aggregated (Wegge & Larsen 1987).

The display behavior, both vocalization and body posture, has been well described based on direct observations (e.g., Hjorth 1970, Müller 1974). From VHF telemetry, the social organization and spacing behavior during daytime, when they are not at the display ground, have also been described (Wegge & Larsen 1987, Eliassen & Wegge 2007): after early morning display, the males retreat to more or less exclusive daytime ranges extending > 600 m out from the lek center. Originally, these ranges were referred to as daytime territories (Wegge & Larsen 1987). However, substantial range overlap has later been recorded on big leks (Storch 1997, Wegge *et al.* 2003), therefore not qualifying for the strict "territory" terminology. Instead, using vocal playbacks, Wegge *et al.* (2005) showed that only a smaller part of the daytime range functioned as an exclusive area, i.e. outside this core area neighboring males shared ranges but tended to avoid each other temporally.

Although much information now exists on Capercaillie males' spacing behavior outside the display territories on the lek, virtually no quantitative information exists on their movements to and from the lek center, or on how they are spaced and move around while they are on the lek. According to the literature, on exploded leks inter-male distances are supposedly long, but birds should be in visual or auditory contact with each other so as to facilitate behavioral interactions (Höglund & Alatalo 1995). However, few quantitative data on the distances between attending males have yet been reported, either for Capercaillie or for other comparable lekking species with exploded lek system. The only studies that report quantitative relationships among attending males are those discussed by Morales *et al*. (2001), based mainly on data collected on the Little Bustard *Tetrax tetrax* (Jiguet *et al.* 2000). Thus, distinguishing exploded leks from the more common classical (or arena) type leks often has been arbitrary and not based on quantitative criteria. The purpose of this paper is two-fold: 1) to provide quantitative information on the spatial arrangements and movements of males when they are actively displaying on the lek, and 2) to

Table 2. Information on Capercaillie males at two leks at Varaldskogen, Norway, during 2009–2011, and number of useful GPS positions.

| | | | | | | | GPS readings | | |
|---|---|---|---|---|---|---|---|---|---|
| Lek name | Year | Male ID | Weight[1] | Beak size[2] | Age[3] | Breeding | Useful (%) | Error[4] | Total[5] |
| Lek A | 2009 | 140 | 4.6 | 28.0 | ≥ 3 yrs | No | 2,114 (*96*) | 88 | 2,202 |
| | | 160 | 4.4 | 28.4 | ≥ 3 yrs | No | 1,763 (*94*) | 113 | 1,876 |
| | | 120 | 4.2 | 24.8 | 2 yrs | No | 2,031 (*93*) | 153 | 2,184 |
| | 2010 | 140 | n/a | n/a | ≥ 4 yrs | A few hens[8] | 1187 (*92*) | 103 | 1290[6] |
| | | 120 | n/a | n/a | 3 yrs | No | 769 (*84*) | 146 | 915[7] |
| Lek B | 2011 | 110 | 4.6 | 27.9 | ≥ 4 yrs[9] | Yes | 1,923 (*85*) | 339 | 2,262 |
| | | 100 | 4.3 | 27.5 | ≥ 3 yrs | No | 1,594 (*70*) | 683 | 2,277 |

1) Total body weight in spring, excluding backpacks (kg).
2) Depth of beak (mm) just behind nostrils (see Moss *et al.* 1979).
3) Age estimated from beak measurement (see Wegge & Larsen 1987).
4) Low quality readings excluded due to no or few contacts with satellites (< 4 satellites).
5) Total readings obtained, excluding those recorded during the off-lek seasons.
6, 7) Fewer total readings because GPS unit shut down too early.
8) Courted a few receptive females and probably mated them, but was not main breeder.
9) Known ≥ 3 yrs in 2010.

describe the general movement pattern of males between their daytime ranges and their display territories on the lek. The terminology and definitions used in this paper for the different parts of the lek are summarized in Table 1 (see also Fig. 1).

## 2. Material and methods

### 2.1. Study area

The study was conducted at Varaldskogen in southeast Norway (60°10'N, 12°30'E) during the springs of 2009–2011. Dominated by a mixture of Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*, the state-owned forest is subject to commercial forestry by the clearcutting harvesting method. The fauna is typical of boreal forests, with recently re-established large carnivores and a dense population of moose *Alces alces*. Main predators on adult grouse are red fox *Vulpes vulpes*, pine marten *Martes martes* and goshawk *Accipiter gentilis*. Spring density of Capercaillie is 2.0–2.5 birds / km$^2$, with small leks – none with > 10 attending males – typically located about 2 km apart. For more detailed information, see Wegge & Rolstad (2011a).

The leks are located in a rather wide range of forest habitats, mostly within older pine forest, but during later years some new leks have become established in middle-aged, thinned stands (Rolstad *et al.* 2007), as also reported from Finland (Sirkiä *et al.* 2010, Miettinen *et al.* 2009). A characteristic feature is that the Capercaillie tends to display in small forest clearings and bogs and on ridges and small hilltops in the forest (Valkeajärvi & Ijäs 1986, Rolstad & Wegge 1987, Helle *et al.* 1994). Of relevance for this particular study, it should be noted that the topography of our studied leks was slightly undulating, and that they were situated in medium-aged and old conifer forest with a relatively open understory, where the visibility of neighboring displaying males was limited to ca. 30–70 m.

In Varaldskogen study area, most females visit the leks for mating during a 6–8 day period in late April (Wegge *et al.* 2010). While attending the lek, they usually relocate by flying in groups when assessing displaying males, for then to descend from the trees just a few days before mating (authors, pers. obs).

### 2.2. Field methodology and programming

Males were captured in ground nets (e.g., Wegge & Larsen 1987) on two leks and fitted with backpacks containing VHF transmitters (142 MHz frequency) and GPS units (Telemetry Solutions,

Table 3. Characteristics of the spacing pattern of lekking Capercaillie males at two leks at Varaldskogen, southeast Norway, during April 20–30, 2009–2011. Medians are pooled values of 7 GPS male seasons at two leks.

| | Median | Range | *N* |
|---|---|---|---|
| Size of lek area (ha) | | 6 and 15 | 2 |
| No. of attending males [1)] | | 4 and 7 | 2 |
| No. of attending females | | 8 and 12 | 2 |
| Size of display territory (ha) | 2.0 | 1.2–5.5 | 7 |
| Overlap of territories (%) | 16 | 12–43 | 4 |
| Size of display site ($m^2$) | 182 | 107–2,342 | 25 |
| Proportion of positions within display sites (%) | 40 | 29–47 | 7 |
| Areal proportion of display sites (%) | 4.4 | 2.5–12.7 | 25 |
| Distance between neighboring males' display sites (m) | 116 | 64–212 [2)] | 5 |
| Distance of excursions (m) | 243 | 72–550 | 34 |
| Number of interactions [3)] | 6 | | 5 |

1) Excluding temporary yearlings.
2) Excluding a case where #120 and #160 used the same display site at two different mornings.
3) Number of incidents when two males were GPS positioned < 10 m apart during three consecutive readings.

Concord, CA, U.S.A.). With VHF included the backpacks weighed 60 g and had a storage capacity of ca. 2,200 positions. The males were captured and instrumented before the females arrived at the leks for mating, and they were recaptured in late summer for downloading of the GPS positions and for changing of backpacks. Information on the sample birds and number of useful positions is given in Table 2. On both leks, other unmarked males were also present. Their locations and general activity areas were recorded and mapped by trained observers staying overnight at the leks during most of the lekking season.

Because the main purpose of this study was to record movements and spacing behavior related to lekking activity, we programmed the GPS units to take positions (fixes) as frequently as every 2 and 3 minutes when the birds were on the lek. Because we also wanted to know their movements to and from their display sites on the lek, we programmed also these periods with short time intervals. Lastly, for mapping their range use during spring and their general seasonal ranges, we programmed the units to take more widely spaced fixes during the whole year. The frequent recording at leks quickly exhausted the storage capacity of the units. Hence, the time periods when data were collected while birds were active and displaying on the lek were restricted to 7–12 days around the peak of mating.

Before deploying the backpacks, we examined the accuracy of the GPS positions by placing the backpacks on the ground at known locations, both in open ground and under a canopy of trees. When recording a fix, the accuracy of GPS positions varies with the number of satellites that the units connect to. Owing to the frequent interval of fixes to be taken on the birds on the lek, the time when the units could search for satellites (timeout) was restricted to maximum 60 seconds. This led to a slightly lower accuracy than the potential maximum of the units. From our field testing we concluded that the units recorded GPS positions at an accuracy of radius < 14 m in dense forest (10 sites, 95% of 339 fixes, canopy cover 100%) and < 5 m in more open ground (25 sites, 95% of 285 fixes, canopy cover < 30%) when they connected to ≥ 4 satellites. Most of the display activity was performed at sites with < 30% canopy cover. Although the technical performance of all the GPS units was not satisfactory, they generated good data, with a total capacity of ca. 2,200 positions per unit. Prior to analyses, 4–30% of the readings were removed either because no position was achieved or because the spatial precision was to low (< 4 satellites) (Table 2; see Wegge & Rolstad 2011b for more details). After downloading, the GPS positions were carefully checked against field notes and map sketches from the observers at the leks, confirming that there were no systematic errors in the readings. When examining male interactions on the lek, we checked consecutive fixes to ascertain the locations of the birds (Table 3).

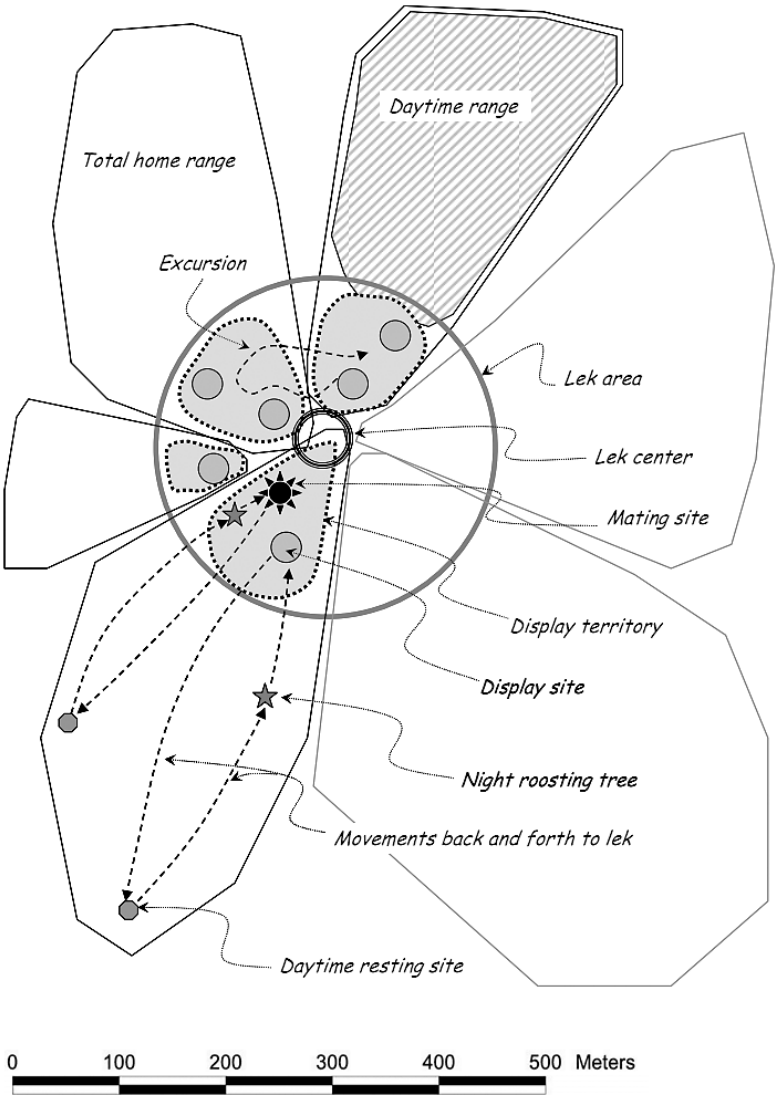


Fig. 1. A general outline of the spatial pattern of lekking Capercaillie males in spring, modified from Wegge & Larsen (1987). Daytime ranges have been drawn to half the scale to enhance readability of the lek area.

### 2.3. Spatial data analysis

The spatial data were analyzed by calculating fixed kernel home range utilization distributions (Worton 1989) from digitized maps, using ArcView GIS 3.3 software (ESRI Inc., Redlands, CA, U.S.A.) and the ArcView extension Animal Movement (Hooge & Eichenlaub 2000). The size of the kernel home ranges is sensitive to the selected smoothing factor and the probability of the utilization distribution. After several test calculations to ascertain appropriate area delineations, we selected a probability of the distribution of 75%, and smoothing factors of 40 when calculating the display territories and 5 for the display sites. To exclude movements back and forth from the daytime ranges, we used a time window from 5:00 to 7:00. Excursions were defined as movements > 50 m directed into neighboring males' territories. Ground movement to and from the lek, as opposed to flying, was defined as a displacement rate of < 50 m / min.

### 2.4. Statistical analysis

Differences between continuous variables were tested with ANOVA and Bonferroni–Dunn post-

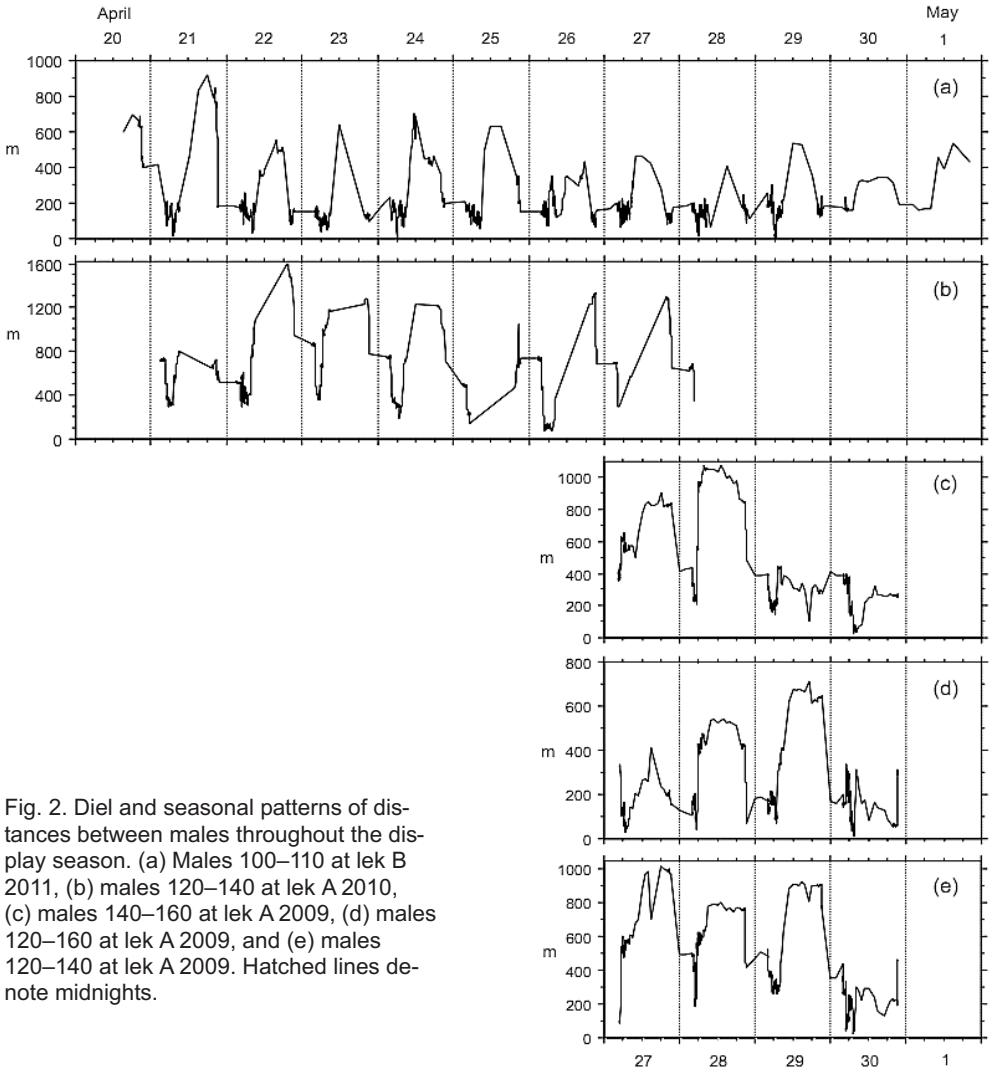


Fig. 2. Diel and seasonal patterns of distances between males throughout the display season. (a) Males 100–110 at lek B 2011, (b) males 120–140 at lek A 2010, (c) males 140–160 at lek A 2009, (d) males 120–160 at lek A 2009, and (e) males 120–140 at lek A 2009. Hatched lines denote midnights.

hoc tests and frequencies of categorical variables were tested with $\chi^2$ and Fisher's exact tests. Seasonal trend lines were fitted using least square locally weighted regressions (LOWESS) with a tension parameter of 33% and tested using Spearman's rank correlations. All analyses were done using the StatView 5.0 software package (SAS Institute Incorporated, Cary, North Carolina).

## 3. Results

### 3.1. General spacing

The lek system of Capercaillie is schematically outlined in Fig. 1. During daytime, the males resided within radially extending ranges (300–1,000 m) from the lek, spending most of their time in ground resting sites at different locations within the daytime range. They commuted to the lek in the evening or early morning, spending the night in repeatedly used roosting trees on or near their display territory, for then to descend and perform morning display at one or more preferred display sites within their display territory. Usually they returned to their daytime ranges in late morning. Owing to a spaced-out pattern during daytime and movement to centrally located territories for display, the distance between neighboring males varied in a regular fashion during the 24-hour cycle (Fig. 2 and 3).

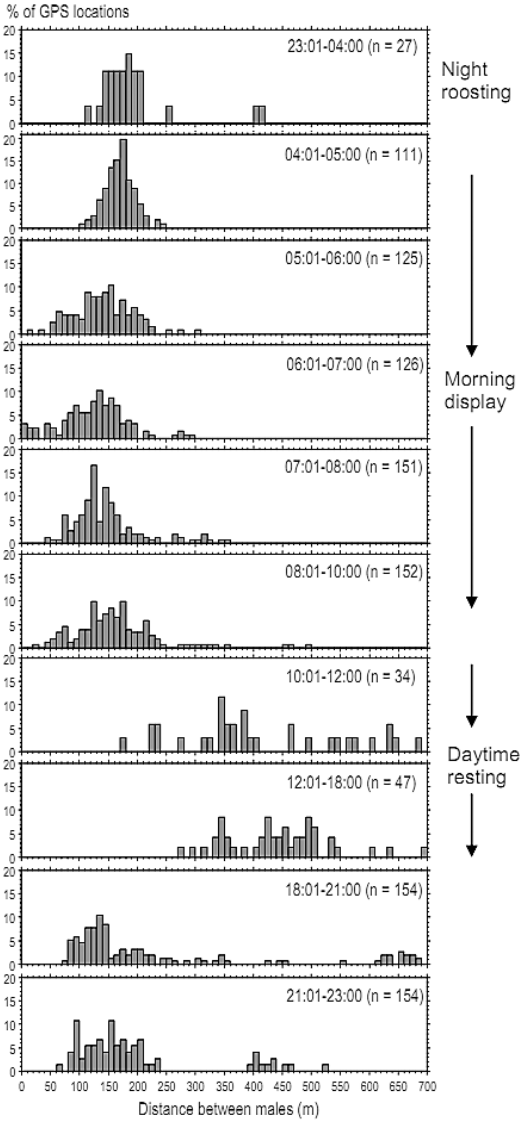


Fig. 3. Daily pattern of the distance between neighboring male 100 and the breeding male 110 at lek B during April 21–30, 2011. GPS position intervals were 3 min. during 04:00–09:00 and 20:00–22:00, 10 min. during 10:00–12:00 and 16:00–18:00, and 1 h. during the rest of the day. Number of positions in brackets.

### 3.2. Spatial arrangement on the lek

A summary of the spacing pattern and movement of the GPS-marked males while on the lek is given in Table 3. The more or less exclusive display territories ranged 1–6 ha (median 2 ha). During the regular advertising display period, each male spent 30–50% of its time displaying on small, well-defined display sites (median 182 $m^2$) within 3–13% of their territories (Fig. 4). When on their display sites, neighboring males were 64–212 m apart. Thus, the display sites were spaced out with ca. 70% of the ground between neighbors being unoccupied. However, during the 2–4 hour long morning display periods, the males moved across most of their rather large display territories. Thus, during the morning the distance between neighbors varied greatly and the males often approached each other within < 50 m distance (Fig. 2).

As the display season progressed, the males positioned themselves increasingly closer to the lek center (Fig. 5). During the days before mating, the daytime occupancy centers were located 580 m from the lek center; after mating this distance was markedly shorter, reduced to a mean distance of 260 m. Similarly, during premating the males often night-roosted outside their display territories on the lek (52%); during and after the mating period they roosted nearly always (92%) on their territories on the lek. The breeding male on lek B (♂110) roosted on his territory where he mated during the whole season (Fig. 5).

### 3.3. Movements

From their display sites, where they spent most of their time, the males often made exploratory excursions into other males' territories, sometimes crossing them, without vocalizing before returning to their own display territory (Fig. 6). Such long-distance movements occurred on average every second day and the direction was frequently diverted towards females when these were present on the lek. The longest distance moved during one morning was 550 m. Occasionally, these excursions resulted in close encounters and fights. During 30 paired male–male recorded mornings over a 10-day period, males were within 10 m of each other 6 times (Table 3); a minimum of 3 of these encounters resulted in physical fights (authors, pers. obs.).

When the females arrived at the lek and had selected one of the males for mating, there was a clear tendency for the other males to move closer to the mating male, often invading his display ter-

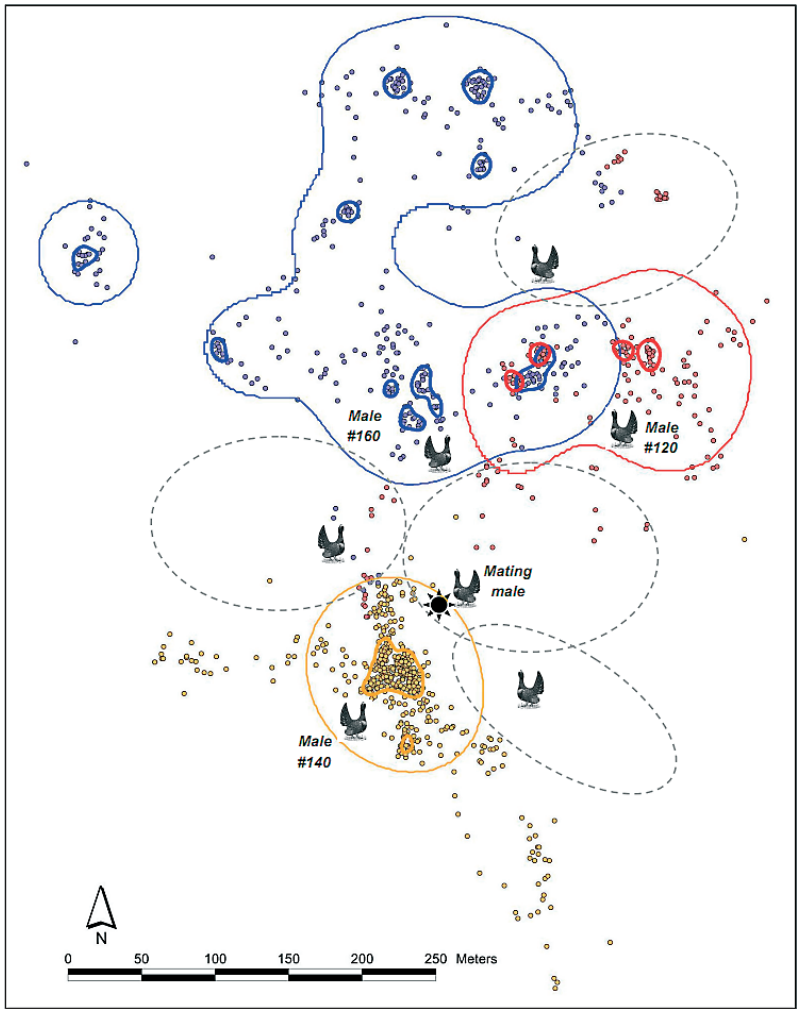


Fig. 4. Spacing pattern of males 120 (red), 140 (yellow), and 160 (blue) during morning display between 05:00 and 07:00 at lek A during April 21–30, 2009 (colored only in electronic version). GPS position interval was 2 min. Display territories are drawn with thin lines and display sites with thick lines. Display territories of four unmarked males are indicated with hatched lines and mating center with a black star.

ritory and approaching him and the females at close distance (Fig. 6 and 7). Hence, the inter-male distances also decreased. However, after mating, they returned to their previous display sites within their own territories.

The males arrived at the lek both in the evening and in the early morning, by either walking or flying (ca. 50 / 50) (Table 4). When departing after morning display, they did so by walking more often (79% of the time) compared to when they arrived at the lek in the evening (walking 54% of the time), and walking speed in the morning was much slower than in the evening (Table 4). Commuting distances to and from the daytime resting sites varied between 150 and 1,000 m. The males traversed the same general area each time, but the paths varied somewhat depending mainly on the starting/ending points within their daytime ranges. An example of the daily movement pattern is given in Fig. 8.

## 4. Discussion

In this study of Capercaillie leks, display territories of 1–6 ha size and males spaced > 50 m apart were much larger than reported for classical lekking species. For instance, in black grouse, male territories on the lek are generally only ca. 10 m apart (Hglund & Alatalo 1995). However, in spite of long inter-male distances and forested habitat, clearly the Capercaillie males displayed at audible

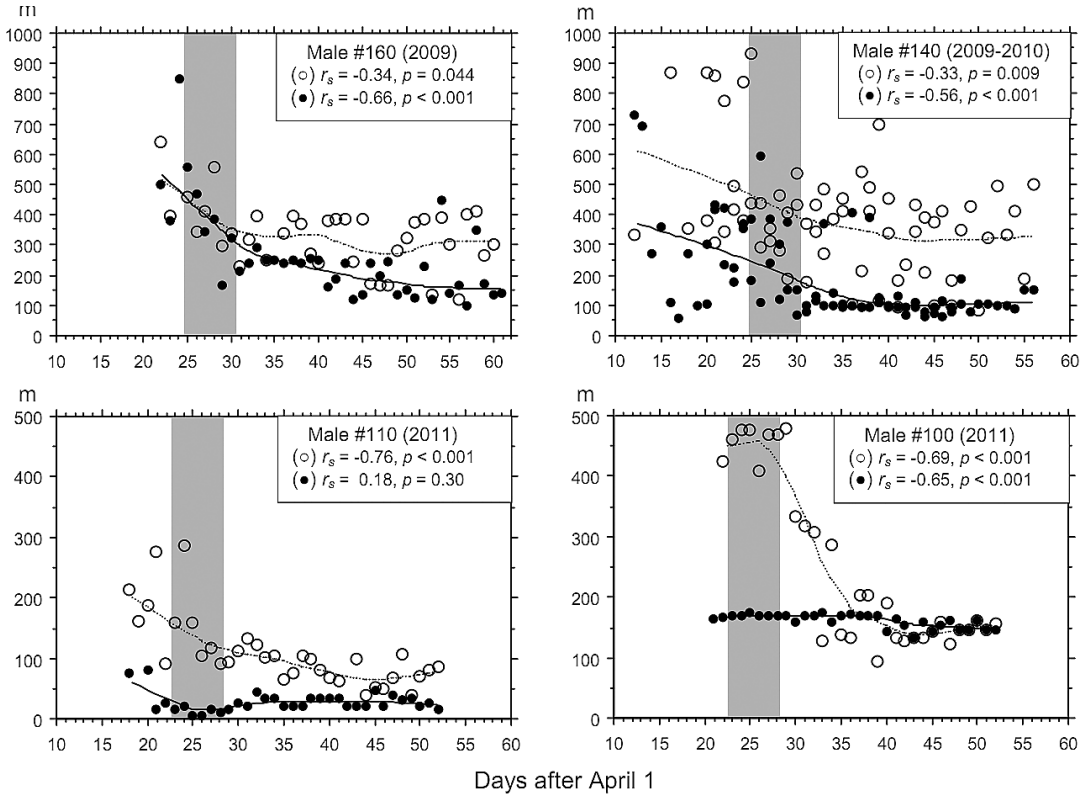


Fig. 5. Distance from daytime resting site (o) and night roosting tree (●) to the mating center at the lek during the display season. Males 140 and 160 were at lek A and males 100 and 110 (breeding male) were at lek B. Mating periods are shaded. Trend lines are least square fitted locally weighted regressions (LOWESS) with a tension parameter of 33% and $r_s$ are Spearman's rank correlation coefficients between distance and time. (Male 120 at lek A had too few daytime positions to be shown).

distances, and often they were also able to see one or more of their neighbors. In many ways, the spacing arrangement was clearly "lek-like" with males interacting with each other, resembling what has been reported from other species classified as exploded leks (Alonso 2000, Morales *et al.* 2001).

Females visited the leks for mating during a week in late April. After selection of breeding male they stayed for 2–4 consecutive days in a group on his display territory. During the peak of mating, neighboring males contracted towards the mating center, frequently staying at 20–50 m visi-

Table 4. Characteristics of the commuting movements of Capercaillie males between their daytime resting sites and their display territories at the lek. Means are pooled values of 7 GPS male seasons at two leks.

| Movements: | Flying/ Walking (%) | Distance moved (m) mean (SD) | Walking speed (m/min.) mean (SD) | *N* |
|---|---|---|---|---|
| Arriving at lek in the evening (roosting within display territory) | 46 / 54 * | 454 (200) | 12.3 (6.4) [a] | 35 |
| Arriving at lek in the morning (roosting within daytime range) | 48 / 52 | 256 (139) | 19.4 (6.6) [b] | 24 |
| Leaving lek in the morning | 21 / 79 * | 434 (174) | 6.1 (2.8) [c] | 37 |

*) Difference between arriving in the evening and leaving in the morning: Fisher's Exact test: $p$ = 0.045 (birds combined).
a, b, c) All comparisons different $p$ < 0.001 according to Bonferroni–Dunn post-hoc test.

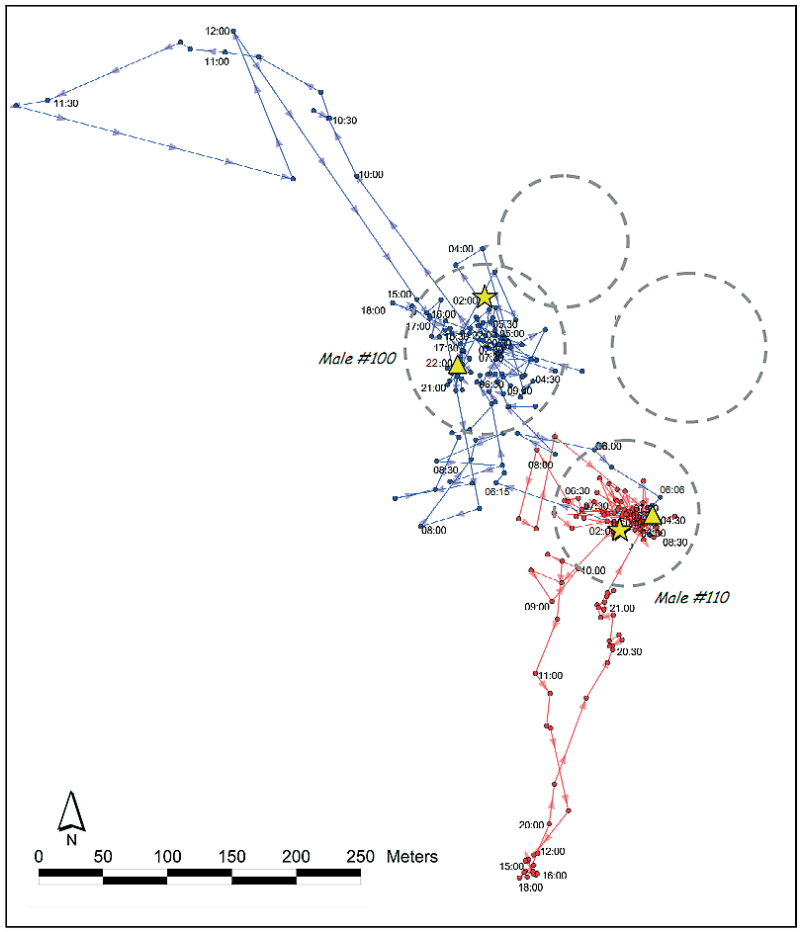


Fig. 6. Movements of breeding male 110 (≥ 4 yrs old, red) and male 100 (≥ 3 yrs old, blue) at lek B during 02:00–22:00 on April 24, 2011, when mating took place (colored only in electronic version). Location of display territories of two unmarked males shown to the north and northeast. Roosting trees are marked with yellow stars in the morning and yellow triangles in the evening. Mating site was at the center of 110s territory. GPS position intervals were 3 min. during 04:00–09:00 and 20:00–22:00, 10 min. during 10:00–12:00 and 16:00–18:00, and 1 h. during the rest of the day.

ble distance. This closely resembles the behavior of female Greater Sage Grouse *Centrocercus urophasianus*, which also spend several days in groups around breeding males before mating (Hartzler & Jenni 1988). In polygynous forest grouse, such behavior of the females has not been reported, although spatial clumping of displaying males has been indicated in both the Ruffed Grouse *Bonasa umbellus* (Archibald 1976), the Spruce Grouse *Canachites canadensis* (Ellison 1973, Herzog & Boag 1978), and the Sooty Grouse (*Dendragapus fuliginosus*) (Lewis 1985), including the Siberian Spruce Grouse *Falcipennis falcipennis* (Andreev *et al.* 2001). Thus, the prolonged and spatially concentrated appearance of females in Capercaillie presumably contributes to males behaving more "lek-like" than the more dispersed displaying North American counterparts, although the pre-mating inter-male distances are not that much different. Although males approached each other, and physical combats did occur (fatal outcomes were observed in previous years), the frequency of spatial interference was rather low, mainly restricted to when males made exploratory trips outside their display territory. Only during the peak of mating did neighbors temporarily abandon their territories and congregate near the mating site; after mating they were again back and displaying from their regular display sites.

As reported in earlier studies (Wegge & Larsen 1987, Wegge *et al.* 2005), neighbors rarely interacted during daytime, as they were then widely spaced. It should be noted, however, that both of our studied leks were rather small (≤ 7 males). With increasing number of attending males (> 30 males have been reported; Blindheim 2008), inter-male distances might be shorter and male–male in-

Fig. 7. The mating site of lek A in 2009, with male 140 in the background and 120 in the foreground. The unmarked mating male is courting two females to the left.

teractions might be more pronounced both on and off the lek. Observations at a large lek (> 25 males) in northwest Russia provided some support for this prediction. Here the daytime ranges of neighboring males overlapped markedly, but the birds avoided each other temporally by spacing out and maintaining minimum distances apart (Wegge *et al*. 2003). Also, when on the lek, the inter-male distances appeared to be shorter than in the present study, presumably because the display territories were smaller (Wegge, pers. obs.). However, habitat structure (micro-topography and vertical vegetation cover) – which affects the visibility along the ground – probably plays an equally or more important role than the number of attending birds. The vegetation cover at the Russian lek was much higher than at the present studied leks. Similarly, in south-central Norway, Rolstad (1989) reported that most displaying males were less than 100 m apart on a medium-sized lek (12–15 males) located in nearly pure Norway spruce *Picea abies* forest with a rather dense canopy and understory cover. Lastly, on a very large lek in northern Norway (> 100 males), in quite open mixed birch *Betula pubescens* and Scots pine forest, Schaanning (1916) reported that the males were spread out over quite a large area; in 1979 the second author visited this extraordinary lek and noted that the displaying males were farther apart than at the smaller leks in the present study. Hence, although the actual inter-male distances among attending males vary both with lek size and habitat conditions, the general pattern remains the same: relatively large display territories on the lek, leading to a spaced out pattern of attending birds, and avoidance behavior during daytime.

The number of birds in our sample was low, consisting of only five different birds, two of which were observed during two lekking seasons. Their behavior was remarkably similar. Only one male (♂160 on lek A in 2009) deviated somewhat by moving over a larger territory with more display sites than the others (Fig. 4). This bird was especially aggressive when captured and was observed more frequently in fights than other males. He was clearly an adult, but not the dominating breeding male on lek A.

Unlike species of classical leks – including the Greater Sage Grouse – Capercaillie males maintained a distance to neighbors also when off the lek, walking long distances within discrete daytime ranges to and from the lek area. While walking away in the morning, they often emitted the "belching" sound (*sensu* Hjorth 1970) with their tails erected (authors, pers. obs.). This behavior, coupled with spatial avoidance and dominance behavior within the core areas of the daytime ranges (Wegge *et al.* 2005), suggests a form of territorial behavior directed either towards recruiting younger competing males (Eliassen & Wegge 2007),

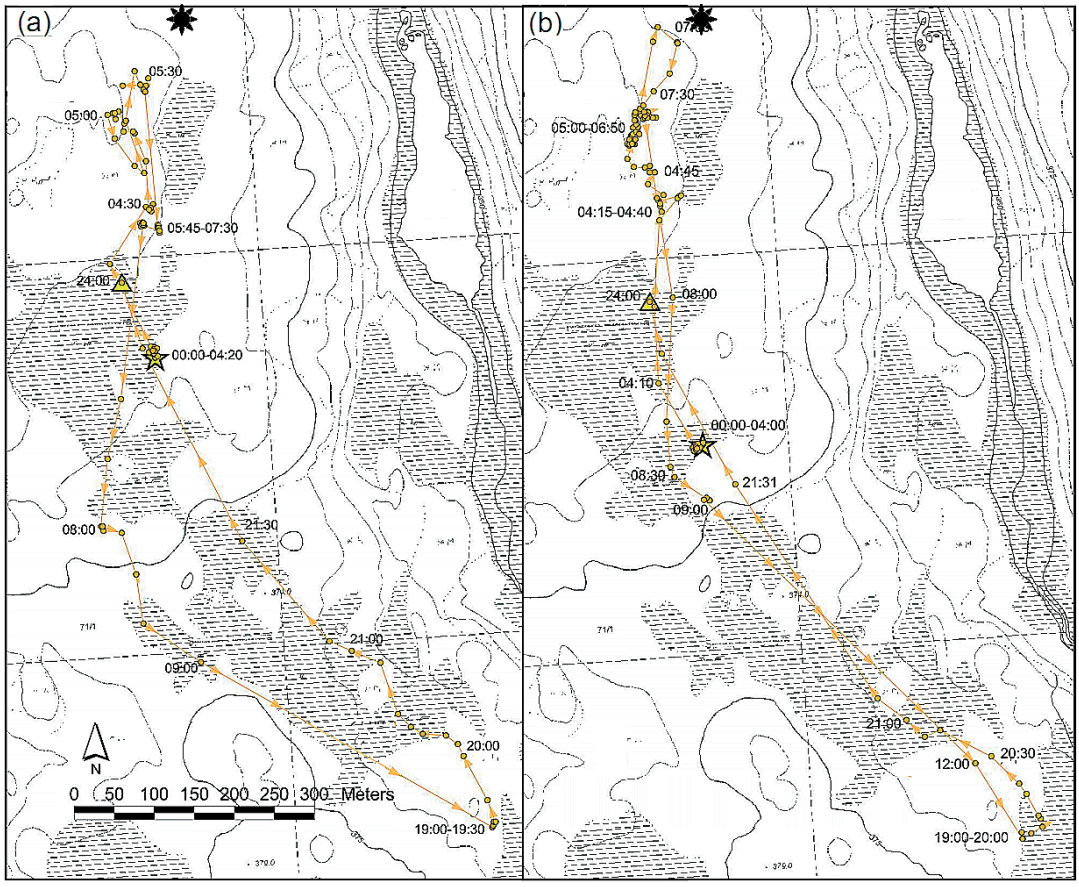


Fig. 8. Movement pattern of male 140 to and from lek A during April 22 (a) and 24 (b), 2010. GPS position intervals were 3 min. during 03:00–07:00, 10 min. during 07:00–09:00 and 19:00–21:30, and 1 position at 00:00, 12:00, and 22:00. Contour intervals are 5 m and hatched areas are open bogs with scattered pine trees. The mating center is indicated with a black star and roosting trees are marked with yellow stars (mornings) and triangles (evenings).

for monopolizing females that have not mated on the lek center earlier in the morning, or for intercepting females that return to the lek for remating. Hence, the daytime ranges appear to function as extensions of the birds' morning display territories on the lek.

Our results place the Capercaillie mating system between the classical arena type with highly clustered males and those with dispersed territories of most other forest grouse. The lek-like spatial arrangement with clustered and interacting males, especially during the mating period, resembles true lekking species, whereas the spaced out pattern and long inter-male distances during most of the display season compares closely with other polygynous forest grouse. As such, the term "exploded lek" seems quite appropriate for the mating system of this species.

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## Tjädertupparnas rumsliga fördelning på "exploderade lekar" granskad med GPS-telemetri

I tjäderns parningssystem spelar tupparna längre ifrån varandra än hanarna på klassiska lekar, vilket

på engelska har benämnts *exploded lek*. Emellertid har varken avstånden mellan tupparna eller deras förflyttningsmönster kvantifierats närmare. Åren 2009–2011 studerade vi den rumsliga fördelningen av tjädertuppar på två lekar i sydöstra Norge med hjälp av GPS-telemetri. Parningscentret var omgett av mer eller mindre icke-överlappande spelterritorier (median 2 ha), men tupparna höll sig största delen av tiden på mindre, avgränsade spelplatser (median 182 $m^2$) innanför sina territorier. När tupparna befann sig på dessa var de inbördes avstånden mellan grannarna 64–212 m. Avstånden minskade till ett minimum under själva parningen. Ibland gjorde tjädertupparna långa exkursioner (median 243 m) som gick över grannarnas territorier; några gånger ledde dessa till interaktioner och närkontakt mellan grannar (< 10 m).

På dagtid var tupparna solitära och höll till på radialt utformade dagområden inom 1 km från lekens centrum. På kvällen och morgonen flög eller gick tupparna till fots till och från leken; oftast till fots när de lämnade leken på morgonen. Avstånden från lekens centrum till övernattningsträdet och till den dagtida uppehållsplatsen avtog genom hela speltiden. Eftersom tjädertupparna är i kontakt med varandra på leken och det rumsliga fördelningsmönstret är ett mellanting av klassisk lek och solitärt spel (utspridd polygyni), passar begreppet ”exploderad lek” bra för tjäderns parningssystem.

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