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# Social interactions among Capercaillie *Tetrao urogallus* males outside the lek during spring

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Capercaillies have a lek-like mating system, with partly overlapping male daytime ranges extending radially out from smaller display territories at the lek. With VHF telemetry, we studied the spatial interactions among neighbouring adult males (n = 10) of different social status in their overlap zones outside the lek. In addition, we recorded responses to display sound that was broadcasted on the lek and in the daytime ranges. All males, irrespective of social status, responded aggressively to the playback when on their display territories on the lek. While in their core areas during daytime, only 2 males, known to be breeders, responded aggressively; others were activated, but not aggressively. When outside their daytime core areas, playbacks elicited less response among all birds. Close encounters (< 300 m apart) within core areas resulted in one male leaving: beta males always left when inside alpha's core area, whereas in 4 out of 9 instances alphas left when inside beta's core areas. The results suggest that the territorial system at the lek grades into a combination of hierarchical and site-related dominance outside the lek. Daytime ranges may consist of exclusive core areas, surrounded with space shared with neighbours where subdominants avoid close spatial contact with those of higher rank. Owing to strong site fidelity and large minimum tolerance distance, the dominance hierarchical structure produces a spaced-out distribution of individuals, which at lower densities gives the appearance of daytime territories.

## 1. Introduction

Among avian subfamilies, the range and gradation of social organizations and mating systems are greatest within the Tetraonidae, the grouse species (Wiley 1974). Many are polygynous with a lek mating system, with males displaying on defined territories on lekking grounds (de Vos 1979, Johnsgard 1983, Höglund & Alatalo 1995). After display and territorial behaviour in the morning, the males leave the lek. Little is known about their social organization during daytime. Among those for which data exist, territorial and agonistic behaviour is replaced by a system of social hierarchy or mutual tolerance (Höglund & Alatalo 1995).

Territoriality and social hierarchies represent two extremes of dominance relationships. Forcing a range of social systems into one or a few categories limits our understanding of both the role of behaviour in resource allocation and of the animals' adjustment to ecological variables (Lott & North 1998). The combined influence of ranking and location has rarely been considered explicitly. In particular, little is known about asymmetries in territorial relationships on leks and on-site dependent dominance among males outside the lek (Wiley 1991).

The large, polygynous Capercaillie (*Tetrao urogallus*) of the boreal forests in the Palearctic has a lek-like mating system (Hjorth 1970, Wegge & Larsen 1987), regarded as intermediate between classical lekking as seen in Black Grouse (*Tetrao tetrix*) and species with dispersed territories such as Spruce Grouse (*Dendragapus canadensis*) (Hjorth 1970, de Vos 1979, Oring 1982). At the lek, the social organization of Capercaillie males deviates from classical lekking species mainly because inter-male distances are longer, although well within auditory and normally within visual contact, and because they occupy relatively large display territories (Lumsden 1961, Hjorth 1970, Wiley 1974, Müller 1979).

In Capercaillie, yearlings and a proportion of the two-year-olds visit more than one lek in a season, and they do not establish discrete display territories at the lek. Older males return to the same lek and display sites in successive years, and after morning display they retreat to more or less exclusive home ranges within 1 km of the lek centre (Wegge & Larsen 1987, Storch 1997). Earlier studies suggested that these 20–60 ha home ranges could be termed daytime territories (*sensu* Davies 1978) due to their non-random distribution and relatively small spatial overlap (Wegge & Larsen 1987, Storch 1997). Recent studies of large leks (Germany: Storch 1997, Russia: Wegge *et al.* 2003) showed that there is substantial spatial overlap between neighbours on such leks, thus suggesting that territorial behaviour is lax when birds are not displaying at the lek. However, strong site tenacity among individuals in successive years and rather dispersed distribution suggest that Capercaillie deviates notably from other lekking grouse in their social structure when they are off the lek during daytime.

In this study, we report the temporal interactions among resident, neighbouring Capercaillie males during daytime based on the locations of radio-marked birds and their behaviour triggered by acoustical playback experiments. Our aim is to examine the hierarchical and territorial components of the spatial distribution among Capercaillie males when they are off the lek, and social interaction among males during the mating season.

## 2. Material and methods

### 2.1. Study area

Fieldwork was conducted at Varaldskogen in southeast Norway, a typical Scandinavian boreal forest dominated by a mixture of Scots Pine *Pinus silvestris* and Norway Spruce *Picea abies*, elevated 200–400 m.a.s.l. Presumably due to habitat fragmentation by commercial forestry (Wegge *et al.* 1992), spring density of Capercaillie was less than 1 displaying male/km$^2$, with leks confined to the remnant patches of later successional forest stages. Snow normally covered the ground when most females visited leks 4–6 days for mating during the last week of April. Main predators were Red Fox *Vulpes vulpes*, Pine Marten *Martes martes* and Goshawk *Accipiter gentilis*. For further description of study area see Wegge *et al.* (1992).

### 2.2. Birds and telemetry

During the springs of 1996 and 1997, 14 males at 6 leks were captured and radio-tagged with transmitters in the 142 MHz frequency range. We recorded morphometric data and assigned each bird to 1 of 3 age classes (viz. 10–11 month-olds termed yearlings, 22–23 month-olds termed two-year-olds, and birds older than 23 months termed adults) according to beak depths (Moss *et al.* 1979) as modified by Wegge & Larsen (1987). Because it is impossible to observe all male–male interactions and breeding activities from hides at a Capercaillie lek, the social status of the radio-tagged individuals was inferred from a combination of observed breeding and observed behaviour and outcome of aggressive encounters with conspecifics.

Males were classified as alpha-males if they were known to have copulated or had won all encounters with conspecifics. Conversely, males that were not observed to have bred and/or had behaved submissively in confrontations with other males were classified as beta-males. Further breakdown of relative dominance at the lek was not attempted.

We determined the precise location of each bird during daytime by triangulations from ground tracking. Mean triangle size of locations used in temporal interactions was 0.058 ha. Most birds were located 1–3 times per day nearly every day during the main lekking period from mid-April to second week of May. Locations were evenly spread throughout the day between 10am and 6pm. Number of displaying males at each lek varied between three and seven.

### 2.3. Playback experiments

In 1997, we conducted playback experiments (n = 44) by broadcasting the display sound of a breeding male that had been recorded with high-quality equipment (Nagra IV taperecorder) at a lek in 1985. The vocal display of Capercaillie consists of three consecutive sounds, referred to as:

(1) The "Clicking-Whetting Canto" (CWC), repeated at short intervals (Hjorth 1970): a double clicking sound lasting several seconds (sometimes minutes). This vocal display escalates into:
(2) A short, abrupt "cork-screw" sound, which is followed by:
(3) A 1–3 seconds high-pitched scraping sound (or sometimes a flutter jump).

In addition, males use a guttural sound ("Belching Cantus" = BC, Hjorth 1970) as an aggressive signal (Müller 1979, Rolstad 1985) when perching in trees in the evening and/or when leaving the lek in the morning.

The display includes ultrasound below 50 Hz, which is at the lower limit of what humans can hear (Moss & Lockie 1979). Analysis of the frequency spectrum of the Nagra recordings in Avisoft-Sonograph Pro (version 2.5, Raimund Spect, Berlin) revealed that the recordings contained frequencies down to 20 Hz. In order to broadcast as much as possible of the low frequency sound, we used a large loudspeaker (Infinity Reference 21i) with frequency range 45 Hz–25 kHz (± 3dB) for the playbacks.

The trials were conducted at the lek (n = 18), in the daytime core areas of individual males (n = 13), and in the peripheral parts of males' daytime home ranges (n = 13). They were selectively directed at 9 radio-marked birds, 4 adult breeders, 4 adult non-breeders and 1 two-year-old at 6 different leks. When setting up the playback equipment in the field, we carefully avoided disturbing the bird and waited a minimum of 30 minutes before broadcasting. The distance to the bird was between 60 and 110 m in the daytime ranges and between 30 and 100 m on the lek. Playback was started after the bird had been inactive for at least 10 minutes, and it was interchanged with periods of silence according to a standardized procedure. The responses of males were classified as follows:

- Withdrew: The male moved away from the loudspeaker when the soundtrack was played.
- Stationary: The male did not change position. We recorded whether the male remained inactive or became active within five minutes of the playback trial.
- Approached: The male approached the loudspeaker during playback, sometimes with aggressive behaviour.

When the birds could not be observed directly, we estimated the response on the basis of variation in the incoming signal from the transmitter. When "inactive" (= no response), the strength of the incoming signal remains constant, whereas when "active" (= response) the strength of the signal changes notably. Before conducting the playback experiments in the field, we tested and calibrated the activity responses by moving the antenna and/or the transmitter by hand in different directions and with changing intensity.

We never performed playback experiments on the same bird more often than every 5 days. To avoid habituation (Kroodsma 1990), the orders of playback locations as well as the sequence of the CWC and BC soundtracks were randomized for each individual. The birds showed no tendency to respond differently after having heard the sound 1 or more times (Cochran-Manzel-Haenzel statistics $Q = 7.45$, $n = 9$, d.f. = 1, $P = 0.59$).

### 2.4. Movement responses at close encounters

The distance between simultaneous daytime positions of 5 pairs of neighbours, 9 adults of different social status and 1 two-year-old, were examined. The median spatial overlap of the daytime ranges of these males, based on 95% Kernel (KER) method (Worton 1989), averaged 30%. A total of 130 paired locations were examined. For males that were observed less than 300 m from each other, the direction and net movement distance were recorded during the succeeding 24 hours. Males either a) left the area to separate areas, b) were located in the same area the following day, or c) one stayed and the other male left the area. A male was said to leave when the distance moved exceeded his average net movement between successive days and/or the new location was physically separated from the first location by a clearcut, pronounced hill, or large, open bog.

The locations of neighbours were related to the area most intensively used by each individual. A male was either 1) inside his own core area, 2) outside both individuals' core areas, or 3) inside the core area of the other male. We noted if it was the resident male (the male in its core area) or the intruding male that withdrew from the area. Core areas were determined by incremental cluster polygons (ICP) based on nearest neighbour distances (Kenward 1987), with an exclusion of 45% of the total number of daytime locations, of birds that were located a minimum of 25 times. The daytime ranges of the monitored males averaged 49.9 ha (95% KER), of which 2.4 ha constituted the 55% ICP core areas. Thus, the core areas, in which the birds spent an estimated 55% of time when off the lek, covered ca 5% of their total daytime ranges.

### 2.5. Statistical analysis

Response to close encounters and playbacks was analysed using Cochran-Manzel-Haenzel (CMH) statistics for repeated measures (Stokes *et al.* 1995). The CMH method addresses the hypothesis of no association between the repeated measure factor (time, location or display sound) and the behavioural response variables, adjusting for the effect of subject (individual).

## 3. Results

### 3.1. Playback experiments

The playback of the "Clicking-Whetting Canto" (CWC) more often elicited active responses than did the "Belching Cantus" (Q = 4.00, n = 9, d.f. = 1, P = 0.046). Hence, when comparing the effect of location we focused on the CWC-trials. Playback of display sound elicited more responses when the birds were on their territories at the lek than when they were inside their daytime ranges (Q = 14.6, n = 9, d.f. = 6, P = 0.024). When at the lek, all adult males, irrespective of social status, responded aggressively by approaching the loudspeaker (Fig.1).

The sub-adult male became active but did not approach during playback. One old breeder physically attacked the loudspeaker when display sound was broadcasted inside his lek territory. At daytime, males tended to respond to playbacks more frequently when they were inside their core areas than when at the periphery of their ranges (Q = 3.60, n = 9, d.f. = 1, P = 0.058). However, responses were neither more aggressive nor evasive when in either area (Q = 0.69, n = 9, d.f. = 1, P = 0.41). When broadcasted in core areas, 2 of the 9 males, both known breeders, responded aggressively. Similar overt aggression was never elicited outside core areas. Most of the birds classified as non-breeders withdrew during playbacks inside their daytime ranges.

### 3.2. Close encounters

A total of 26 close encounters between neighbouring alpha and beta-males were recorded (Table 1). In 8 instances, both males were located inside their own core areas, but within 300 m of each other. The following day, after having attended the lek, they were back in their respective core areas.

In the remaining instances, both neighbours were located at the border or inside the core area of one of the males. During the succeeding 24-hour period, 1 of the males abandoned the core area, while the other remained. In 14 of these 18 situations, it was the beta-males that left, but the observed reaction patterns appeared to be somewhat dependent on the location of interactions

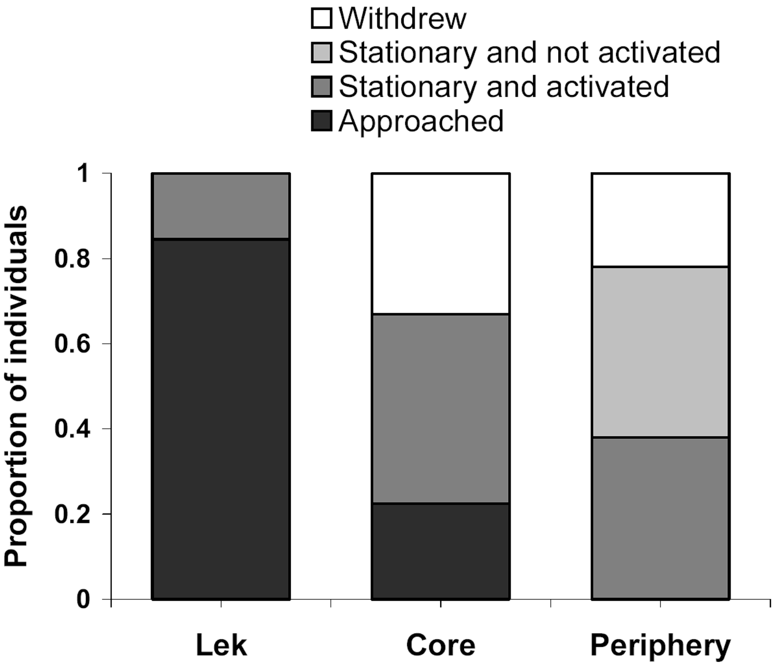

Fig. 1. Reaction patterns of males (n = 9) to playback when display sound (CWC) was broadcasted from within the daytime ranges (core areas and periphery) or inside lek territories.

(Q = 2.67, d.f. =1, n = 10, P = 0.10): When both males were located inside the alpha-males's core area (n = 9), the higher-ranking male always remained. The beta-males either moved back to their own core areas or moved an average distance of 755 m ± 194 m (SE) to a location far outside their ordinary ranges. This type of response was never observed for any alpha-male, but in 4 out of 9 instances of close encounters in the core area of a beta-male, the alpha-male returned to his own core area (Table 1).

## 4. Discussion

In a territorial system, a member is only dominant while on its territory. The playback experiments confirmed that adult male Capercaillie is territorial, irrespective of breeding status, when they attend the lek. When off the lek during daytime, only high-ranking breeders responded aggressively, and most lower-ranking birds withdrew when they heard the display sound track of the alien breeder. At the periphery of their ranges, the playbacks trig-

Table 1. Reaction patterns at close encounters between neighbouring alpha and beta-males during daytime outside the lek.

| Position of birds day 1 | Number of situations | Position next day |
|---|---|---|
| Both inside their own core areas <300 m apart | 8 | Same location |
| Beta-male inside core area of the alpha-male | 9 | Alpha-male always inside his own core area. Beta-male has moved to his own core area (4), or is located far outside his ordinary range (5). |
| Alpha-male inside core area of the beta-male | 9 | Alpha-male still in beta's core area and beta-male outside (5), or alpha-male back in his core area (4) |

Alpha-male = known breeder and/or shown dominant behaviour at the lek. All minimum 4 years of age.
Beta-male = not known to have bred and shown subdominant behaviour at the lek (includes one two-year-old).

gered little or no response among all birds. Clearly, responses diminished with increasing distance from the lekking ground.

The motivation for responding to stimuli may vary between the lek and the daytime ranges. On leks, males frequently interact with each other and aggression level is high. Aggression-related hormones, such as testosterone, change between seasons (grouse: Hissa *et al.* 1987, Hannon & Wingfield 1990), and on shorter time scales they rise during aggressive encounters and decline in less aggressive periods (Wingfield *et al.* 1987, but see Wingfield & Lewis 1993). Hence, the testosterone levels were probably lower during daytime than when the birds were displaying on the lek. Furthermore, the broadcasted sound had been recorded from a dominant male of breeding status (but unknown to the targeted males in this study), and it was somewhat distorted because the low-frequency part could only be partially reproduced (see Methods), possibly also reducing the hearing range of the sound. Combined, these factors probably acted to reduce the responsiveness to the playbacks at daytime. Nevertheless, the fact that males indeed responded aggressively when they were away from the lekking ground, and that only breeding males did so, indicate a high level of aggression towards intruders.

The movement reactions to the nearby presence of conspecifics also showed that males during daytime space themselves more according to a hierarchical structure: non-breeding individuals clearly avoided close spatial contact with breeders. However, the avoidance behaviour appeared to be site-specific: when the lower-ranking male was in his core area he was less inclined to retreat when an alpha was close by, than when he was outside his own core area. The limited data indicate that within their daytime ranges, core areas may function more like exclusive territories, while outside their core areas, the birds adjust their space occupancy hierarchically according to the position and rank of neighbours.

A hierarchical social organization is common among males of lekking grouse species (Höglund & Alatalo 1995). Our results indicate that the gradient in spatial structures within such a broadly defined social system may vary considerably. In Capercaillie, the long minimum tolerance distances and the rather high level of aggression among dominants produce a spaced-out distribution of individuals during daytime. Storch (1997) proposed that the males' activities outside the lek, and hence their spatial arrangement, were an extension of their behaviour on the lek, whereas Wegge & Larsen (1987) considered daytime activities to be directed at energy conservation and thus quite distinct from that at the lek. Although both behaviours are ultimately directed at mate acquisition, the present data support Storch's (1997) suggestion.

In contrast to other lekking grouse species, why do male Capercaillie space themselves out and occupy separate home ranges near the lek, with subdominant males avoiding close spatial contact with those of higher rank? Resource defence is an unlikely cause, not only because of polygyny but also because their staple spring food is plentiful (Borchtchevski 1995, Odden *et al.* 2003). Instead, mate acquisition and predator avoidance are more probable explanations. A wide spacing of aggressive individuals limits the number of competitors and increases the chances of dominant males to detect and intercept females on their way to the lekking ground. Also, being solitary is, in forested habitats, probably a better strategy against predators than flocking, and the strong site fidelity in successive years (Wegge & Larsen 1987, Storch 1997) probably accrues anti-predator benefits to a long-lived bird like Capercaillie.

The results of this study give support to the interpretation that male daytime home ranges are not territories in the behavioural sense of this term, although at low bird density they are largely non-overlapping and thus give the appearance of territories. Instead, the social organization appears to change from a territorial system at the lek to more hierarchical dominance outside the lek. The larger daytime ranges may consist of exclusive core areas with territorial behaviour, surrounded by larger space wherein the birds are more tolerant to the presence of neighbours. As shown by Wegge *et al.* (2003), such a system does not limit the total number of males attending leks and has therefore little regulatory effect on local male density in spring.

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## Metsokoiraiden (*Tetrao urogallus*) sosiaaliset vuorovaikutukset keväisin soidinalueen ulkopuolella

Metson parittelu tapahtuu soitimella. Koiraiden päiväreviirit, jotka naapurimetsoilla menevät osittain päällekkäin, laajenevat säteittäin keskustassa olevilta pienemmiltä soidinreviireiltä. Tutkimme VHF-telemetrian avulla erilaisen sosiaalisen statuksen omaavien koirasmetsojen käyttäytymistä (n = 10) niiden kohdatessa yhteisellä maaperällä soidinreviirin ulkopuolella. Lisäksi nauhoitimme vastaukset soidinääntelyyn, jota lähetettiin soidinalueilla ja päiväreviireillä. Kaikki metsot vastasivat aggressiivisesti soidinääniin, kun ne olivat soidinreviirillään. Kun metsot olivat päiväreviirinsä ydinalueella, vain kaksi varmasti paritellutta koirasta vastasi aggressiivisesti soidinääniin. Muut koiraat reagoivat, mutta eivät aggressiivisesti.

Päiväreviirinsä ydinalueen ulkopuolella nauhoitteet aiheuttivat vaimeampia reaktioita. Lähikohtaamiset metsojen välillä (<300 m) ydinalueilla johtivat poikkeuksetta toisen koiraan poistumiseen. Kaikissa tapauksissa, joissa beta-koiras oli alfa-koiraan reviirin ydinalueella beta-koiras poistui, kun taas alfa-koiraista vain neljä yhdeksästä poistui kohtaamisesta beta-koiraan ydinalueelta. Tämä viittaa siihen, että soitimien reviirisysteemi perustuu sekä reviireihin että yksilöiden väliseen hierarkiaan. Päiväreviirit saattavat koostua tarkasti puolustetuista ydinalueista, joita ympäröi naapurien kanssa jaetut alueet. Näillä alueilla huonommassa asemassa olevat koiraat välttävät kohtaamisia dominoivien koiraiden kanssa.

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