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Lost hotspots and passive female preference: the dynamic process of lek formation in capercaillie *Tetrao urogallus*

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The evolutionary processes behind the polygynous mating system known as leks are difficult to document. One approach is to study the behaviour that drives the formation of new leks today. Several hypotheses have been put forward to explain the formation of leks, and they can roughly be divided into two groups; one which advocates that the males are the driving force and one which argues that the females are the driving force. In this study we use data from a long-term study (1979-1998) of a capercaillie population at Varaldskogen in southeast Norway to develop a model describing how new leks are formed in this species. By using data on spacing pattern and behaviour of radio-marked young and adult birds of both sexes we demonstrate how the situation develops from winter towards mating in spring. Furthermore, we report on a few cases of new leks that have arisen in the area during the 20 years of study. We argue that both female mate choice, male territoriality and male attraction to locations with high densities of females are involved in a dynamic process of lek formation. We present results which indicate that new leks are mainly founded by young birds. Finally, we show that when new leks are formed the spacing patterns of the individuals involved change. This questions the method of using comparisons between the position of female home ranges and established leks to infer how leks are formed.

Key words: capercaillie, hotspots, lek formation, spacing, Tetrao urogallus

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The evolution of lek mating systems seems to depend on non-defensibility of resources and the absence of male parental care (Emlen & Oring 1977). Bradbury (1981) discussed the relationship between male and female spatial dispersion and the defensibility of resources. Based on such relationships Bradbury (1981) and Bradbury & Gibson (1983) put forward two alternative explanations for the formation of leks. The 'fe-

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male-preference' model explains the existence of leks as a result of a female-initiated process: females prefer aggregations of males to facilitate mate choice. In the 'hotspot' model, males are the proximate driving force, and leks are formed when males are attracted to patches with high densities of females. Testing predictions on female range use in relation to leks on the basis of these models has often proved to be difficult, not least because of problems connected with defining prenesting ranges (Höglund & Alatalo 1995). Also, the predictions are not always mutually exclusive for one model or the other (Beehler & Foster 1988).

A few studies (Wegge & Rolstad 1986, Ménoni 1997, Storch 1997) have addressed the question of how leks arise in capercaillie *Tetrao urogallus*. Results supporting the hotspot model were reported by Ménoni (1997), whereas Storch (1997) concluded that the large intraspecific variability in female movements made it difficult to use female home range size as a critical test of lek formation in capercaillie. According to Bradbury & Gibson (1983) the hotspot model would be falsified if male display sites were totally unrelated to areas of maximum female home range overlap. Wegge & Rolstad (1986) presented telemetry data on the spacing pattern of capercaillie in spring. Neither the hotspot nor the female preference model was supported by the data, and the regular spacing pattern of males and leks suggested that male territoriality was more important than female range use in determining the position of leks. Female preference seemed to be of little importance because the size of their spring home ranges was too small compared to the spacing of leks (Wegge & Rolstad 1986). The hotspot model was refuted partly because no relationship was found between male display sites and areas of maximal female traffic in spring. However, later studies on spacing patterns in late winter (i.e. when display activity starts) revealed that female ranges were not unrelated to traditional display sites; females were in fact avoiding proximity to leks at this time of the year (Gjerde & Wegge 1989). These findings suggested a re-evaluation of the relationship between spacing patterns and lek formation in capercaillie.

In this paper we focus on the dynamic aspects of lek formation. Putting together pieces of information from a long-term study on capercaillie we present a picture of how new leks probably arise in this species. We argue that both male territoriality, male attraction to female hotspots, and female preference are involved in the process. We show that range use within an established system of traditional leks may not be appropriate for testing models of lek formation. Furthermore, we document that new leks may be formed by particular population segments which have range uses that differ from the rest of the population.

Methods

The main population study on capercaillie was carried out at Varaldskogen in southeast Norway (60°10'N, 12°30'E; 18,000 ha). In addition, supplementary data on spacing of leks were collected from the Fjella area (59°30'N, 11°30'W; 12,000 ha), 110 km southwest of Varaldskogen. Both areas are typical Scandinavian boreal forests on medium-poor soils dominated by mixed coniferous forest of Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*. The study areas are rather uniform with open bogs and lakes interspersed in an undulating forest landscape elevated 200-400 m a.s.l. The Fjella area mainly consists of mature forest, whereas clear-cuts, saplings and pole stages dominate at Varaldskogen. For further description of the study areas see Wegge & Rolstad (1986), Rolstad & Wegge (1987b) and Gjerde (1991).

Since 1979, a total number of nearly 200 subadult and adult individuals have been radio-marked and monitored all year round, most of them in the main study area at Varaldskogen. Catching, handling, ageing and radio-tracking techniques are described by Wegge & Larsen (1987). Results on spacing of individuals presented here are based on telemetry data from 34 females (488 locations), 16 adult males (406 locations) and nine subadult males (160 locations) collected during late winter (i.e. 1 March - 15 April) in the years 1981-1987 at Varaldskogen (Gjerde & Wegge 1989).

During 1981-1987 the capercaillie spring population at Varaldskogen varied within 0.3-0.9 displaying males/km^2 and approximately twice as many hens (Wegge, Rolstad & Gjerde 1992). For simplicity, we here assume that the mean number of subadult males is equal to the number of adult males (≥3 years old), and that the number of females is twice the total number of males. These ratios are based on mortality data (Wegge, Larsen, Gjerde, Kastdalen, Rolstad & Storaas 1990) and annual spring and autumn censuses.

A complete mapping of leks (i.e. display sites where females are mated) was obtained by checking information provided by local sources, monitoring movements of radio-marked individuals, and systematically searching the remnant areas in late winter and spring. Based on this survey we located 23 lek sites at Fjella and 24 lek sites at Varaldskogen.

In 1986 and 1987, sporadic and temporary display activity during 1 December - 15 April was mapped and

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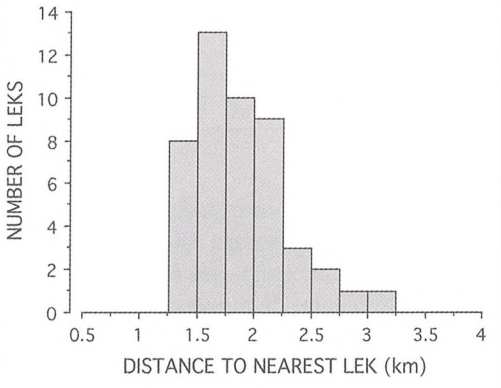


Figure 1. Distribution of the distance to the nearest lek for 47 leks in southeast Norway.

for each incident a detailed sketch was drawn describing the position of tracks, roosting sites, and roosting and feeding trees. Such display activity was recorded by approaching radio-marked birds, and by following tracks in snow. The number of birds of each sex involved were counted. Group size of flushed radio-marked females (N = 102) did not differ from that of randomly encountered females (N = 89), so the material was pooled. Birds were considered to be together in groups if they were closer than 100 m to each other. When snow-tracking, capercaillie display activity was revealed by characteristic jumps and wing marks along the tracks. The length of tracks and their maximum distance from feeding and roosting sites were measured. Pine trees used by capercaillie for feeding and roosting (activity trees) were mapped by searching for droppings and spilled needles in the snow (Gjerde 1990, 1991).

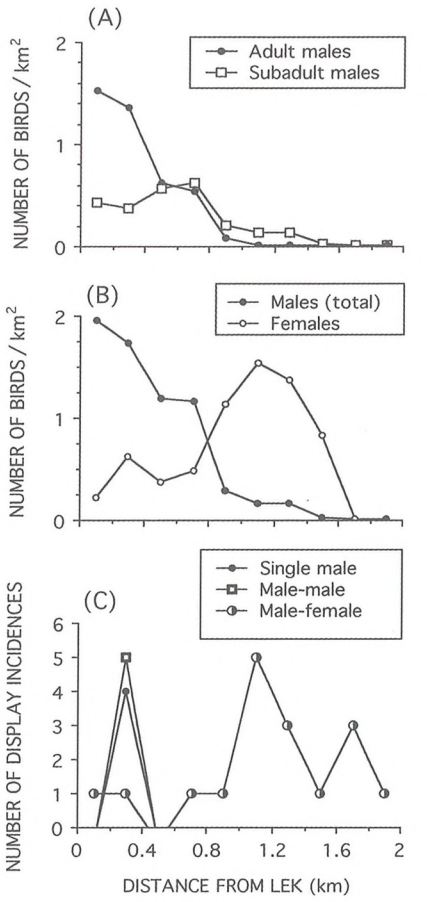


Figure 2. Spacing of radio-marked capercaillie of different age and sex in late winter, and the distance from leks of display tracks recorded by snow-tracking; A): Density of adult and subadult males at different distances from leks; B): Density of all males and females at different distances from leks; C): Relation between the frequency with which display incidents were observed and the distance from leks.

Results

Spacing of leks

The distances to the nearest lek varied between 1.3 and 3.1 km for 47 leks (Fig. 1), and the distribution of the distances was skewed towards the longer distances. The highest frequency of observations was within the interval of 1.50-1.75 km. The distribution indicates a minimum distance of 1.3-1.5 km between neighbouring leks.

Spacing of individuals in late winter

Based on the distribution of radio-fixes relative to leks and the mean density of females, adult males and subadult males, the expected densities of each group at different distances from leks were estimated (Fig. 2A and B). Figure 2 illustrates two important points: 1) in late winter females concentrated in the interlek regions (>800 m from leks) where male density was low, and 2) the few males in the interlek regions were mostly subadult males (81%). The maximum density of subadult males was found between the maxima of adult males and females, approximately 400-800 m from the lek centre. Figure 3 shows the winter home ranges of four radio-marked males around a lek in 1983. A subadult male (2-3 years old) made three recorded visits

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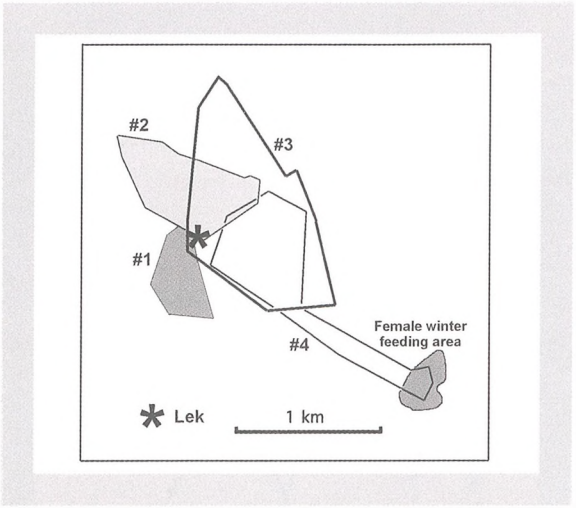


Figure 3. Winter home ranges of four radio-marked males around the lek Torstimäki in 1993. The males (#1 - #4) were >6½ , >4½, 3½, and 2½ years old, respectively. The youngest male (#4) made three visits to a female feeding area situated 1,800 m from the lek centre.

in late winter to a 30-year-old pine plantation, situated approximately 1,800 m from the lek centre (1,300 m from the nearest lek), where a group of 2-4 females were staying at the time. On one of the visits radio-fixes indicated that the subadult male stayed in the area for about one week.

Late winter display activity

At Varaldskogen, mating takes place in late April. However, the first snow tracks of displaying males were found during 15-25 February (data from 1981-1983 and 1985-1987). Ground activity in late winter (15 February -15 April) was recorded by describing 110 female trails and 232 male trails in snow. The mean walking length of such trails was 128 m (range: 2-635 m) for males and 31 m (range: 4-66 m) for females. Short trails of both sexes were usually associated with normal winter behaviour and roosting beneath spruce trees with low branches. However, male trails were longer and more often (21%) found far (>100 m) from feeding and roosting sites than female trails (6%; $G = 13.66$, $df = 1$, $P < 0.001$).

The male snow tracks recorded included display activity at 26 sites in the period 16 February - 12 April in 1986 and 1987. Display activity was recorded as solitary male display, two males displaying, or male(s) displaying at sites with female(s). Display activity was not confined to traditional lek sites. Solitary male or male-male display (35% of the incidents) were all found close to leks, whereas male-female display (65%) was frequently found far from leks (see Fig. 2C). Three male-female display incidents were recorded in late February. If they are excluded, only one (700 m from lek centre) of 14 male-female incidents was recorded closer than 800 m to the lek centre. In the cases of male-male display (N = 5) no roosting or feeding tree sites were found within a distance of 100 m.

Table 1. Frequency with which females, either courted or not courted by males, were observed in groups of varying sizes (1-6). N = total number of females observed.

	Female group size					
	1	2	3	4	5	6
Courted females (N = 36)	4	8	4	1		
Not courted females (N = 145)	62	27	5	2		1

Late winter display activity seems to be particularly directed towards groups of females. Of 36 flushed females that were subject to courting by males, only four (11.1%) were single, compared to 62 of 145 (42.8%) flushed females not courted in the same period ($G = 14.38$, $df = 1$, $P < 0.001$; Table 1). In 16 of 17 cases (94%) the females were courted by a single male. Tracks in the snow and the amount of droppings at roosting sites and beneath feeding trees revealed that males in most cases were visitors with a short stay, and that the female(s) had stayed there considerably longer.

Premature leks

In most cases, late winter display was a short-term event, occurring when individuals came into contact

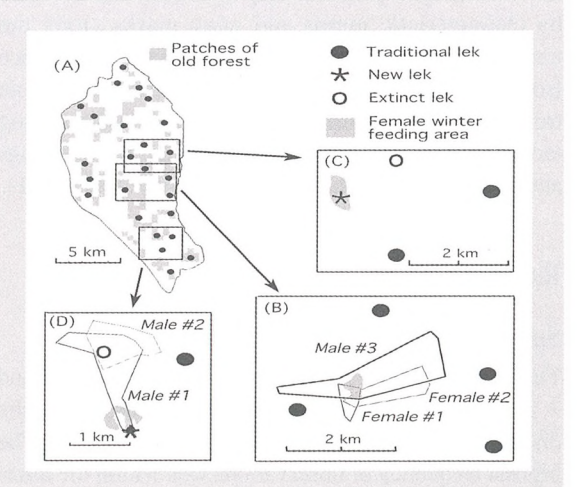


Figure 4. A): The Varaldskogen study area with old forest patches (shaded) and leks (dots). B): A premature lek (no mating) at Svarttjernet with indications of the ranges of one subadult male, one subadult female and one adult female and three neighbouring leks. C): A new lek at Emtberget founded after clear-cutting and relocation of a neighbouring lek at Stormyr. D): A new lek founded at Hockasuo after clear-cutting of half the original lek site at Kockaroinen.

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with each other by chance, or when males made short visits to females in the vicinity of their current place of residence. At a few sites, however, repeated display was observed, resembling the activity at leks prior to mating. In 1987, two radio-marked females and one radio-marked male (among others) were involved in such a situation at 'Svarttjernet' (Fig. 4B). The area was situated between existing leks (1.1 km from the nearest lek) and was dominated by middle-aged (25-35 years old) pine plantations, extensively utilised by females in winter. Sporadic display activity had been observed in the area the previous year. In 1987 display activity was recorded for the first time on 14 March when a radio-marked subadult male (#3) courted two unmarked females. In the beginning of April two radio-marked females (#1 and #2) staying in the vicinity joined the two other females. On 5 April, three males (including #3) courted at least four females (including #1 and #2) in the area. Display activity continued until 12 April, when the lek situation broke up. Female #1 (an adult) moved to the lek where she mated the previous year, 1.1 km west of the area. Female #2 (10 months old) dispersed successively westwards and stayed about 8 km away at the time of mating (late April - early May). Male #3 moved north and eventually recruited into a traditional lek site 2.1 km away.

New leks

Formation of a new lek is a rare event in a capercaillie population. Nevertheless, we were able to record some information about this process at two locations at Varaldskogen. The first example (Fig. 4C) took place in the area 'Emtberget' which is covered by mature mixed coniferous forest that was intensively used by both males (midwinter only) and females during the winters of 1982-1987. The distance between this area and the nearest lek was 1.0-1.6 km. In 1983, an unmarked male courted a group of three females as late as 20 April in the southern part of the area, but all left before mating. In the autumn of the same year, the nearest lek site 'Stormyr' was clear-cut as an experiment. The lek was situated on a 270 ha patch of old forest northeast of Emtberget, and most of the old forest patch was clear-cut. The two following years (1984 and 1985) the lek at Stormyr diminished due to lack of recruitment and moved 800 m eastwards in 1986. In late winter 1987 intensive display activity was recorded within the wintering area at Emtberget, and a new lek developed here during the next two months. At mating time, four males displayed at the lek. In the following years (1988-1993), the size of the lek varied between three and nine displaying males.

The other example also involved experimental cutting. In 1986, two subadult males (both radio-marked) displayed on a small lek 'Kockaroinen' situated on a 64-ha patch of old forest (Fig. 4D). In autumn 1986, approximately half the area of old forest was clear-cut. During the following spring, the oldest male (#1, 2-3 years old) moved around within a large home range courting females at, at least, two sites, and finally succeeded in mating females in a 40-year-old pine plantation at 'Hockasuo', situated 1.8 km south of the original lek. A high density of female feeding and roosting trees showed that this area had been extensively used by females during the preceding months. This new lek site was later used continuously by capercaillie. The youngest male (#2, 1-2 years old) stayed at the old lek and mated females there. However, the next spring this male recruited into a lek population 2.8 km eastwards and the original lek site has not been used since then.

Discussion

The capercaillie mating system

The mating systems of the grouse family range from more or less monogamous species, through intermediate promiscuous systems with dispersed males, to true lekking species.

The capercaillie has apparently been a difficult species to fit into comparative studies of grouse, and has sometimes been labelled a lekking species (e.g. Wiley 1974) and sometimes placed among the species with dispersed males (e.g. Wittenberger 1978). Although individual capercaillie males are spaced farther apart than in most lekking grouse species (Hjorth 1970), recent studies (Wegge & Larsen 1987, Storch 1993, 1997) leave little doubt, in our opinion, that the capercaillie mating system is of the true lekking type. All the criteria for being a lekking species suggested by Bradbury (1981: 138) are normally fulfilled: Males gather and display in spring on less than 1% of the total habitat available, and mating success is highly skewed among males (Wegge & Larsen 1987). Leks are regularly spaced with a mean minimum distance of 2.0 km (Wegge & Rolstad 1986). No leks were closer than 1.3 km and the skewed distribution indicates that this may be a minimum distance (see Fig. 2). The spacing of leks is much more regular than in black grouse *Tetrao tetrix* (Angelstam 1983), sage grouse *Centrocercus urophasianus* (Bradbury, Vehrencamp & Gibson 1989) and greater prairie-chicken *Tympanuchus cupido* (Schroeder 1991). The regular spacing of capercaillie leks is probably related to male range use. The spring home ranges

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of adult males extended 600-1,000 m radially from their display territories at the lek, and 98% of all off-lek locations were within 1 km from the lek centre (Wegge & Larsen 1987). Thus, the distance between leks corresponded to the diameter of two male home ranges, and was largely independent of lek size or population density (Wegge & Rolstad 1986). In our context, it is not crucial whether these spring home ranges were actively defended or not. The important fact is that spring home ranges of adult males from neighbouring leks were contiguous, in accordance with the definition of a territory *sensu* Davies (1978).

Site tenacity is strong in adult capercaillie. Telemetry data have revealed that after becoming an adult, individuals repeat their pattern of movements year after year, although this sometimes imply fairly long seasonal movements (10 km; Rolstad 1989). All adult males and 95% of females visited only one lek during the display season (Wegge & Rolstad 1986, Wegge & Larsen 1987). Furthermore, birds monitored for more than one spring season were, with few exceptions, faithful to their old lek (Wegge 1985, Wegge & Larsen 1987). Subadult males, however, visited 1-3 neighbouring leks before settling at one of them (Wegge & Larsen 1987). They had larger home ranges than adults in late winter (Gjerde & Wegge 1989) and spring (Wegge & Larsen 1987). The site tenacity of adult birds and the recruitment of young birds on existing leks result in a very stable system of leks. The mean lifetime of lek sites was estimated to about 50 years at Varaldskogen (see Rolstad & Wegge 1989) and is probably higher in landscapes that are less affected by forestry.

Lek formation in capercaillie

Tests of the models suggested by Bradbury (1981), Bradbury & Gibson (1983) and Bradbury, Gibson & Tsai (1986) rely on the assumption that the factors determining lek formation are revealed each time lekking arises on a lek site, i.e. each breeding season. However, three levels of events should be recognised: 1) Evolution of lek mating systems, 2) formation of new leks, and 3) yearly phenology of established leks. The spacing of males and females around established leks may not correspond to those present when new leks are formed, as demonstrated in this study. Likewise, one should be careful in assuming that spacing patterns in a specific area today are similar to those prevailing when and where the species evolved its mating behaviour. This may be particularly relevant to lekking species, where 'runaway' processes of sexual selection may allow this mating system to persist even if the initial lek-forming conditions have changed. Obviously, inferring directly from patterns of yearly phenology of established leks to evolution of a mating system is rather dubious.

The present data on capercaillie suggest a strong hotspot component in lek formation. New leks are formed in areas with high densities of females and low densities of males in late winter. New leks arise when males visit females in the inter-lek zones and succeed in keeping them there until mating. These hotspots are later lost and no longer detectable in a system of established leks. When a new lek arises females seem to give up their late winter areas to the males associated with the lek. This pattern is revealed every season as a change in spacing pattern of males and females from midwinter to late winter (Gjerde & Wegge 1989, Figure 2 in this study): when males start to display, females retreat to the inter-lek zones, probably to avoid early courting interference. This shift in range use clearly shows that a stable system of traditional leks may not be appropriate for studying the relationship between range use and lek formation. Instead, the process of lek formation should be studied directly. This would certainly be easier to study in species with leks of less longevity than those of capercaillie.

We know very little about how females react to male courtship outside established leks. We know, however, that in most cases males do not succeed in keeping the females in the area until mating. Formation of new leks were rare events, whereas courtship outside established leks was quite common. This indicates a high degree of female preference in the process of lek formation. However, the female preference observed appeared to be of a passive kind, as females did not move around in search for the best males. Rather, they exerted a preference for mating sites by accepting or (in most cases) abandoning the attempted leks offered in the vicinity of their late winter/prenesting ranges. At Varaldskogen, adult females normally visited only one established lek in spring (Wegge & Rolstad 1986). In contrast, Storch (1997) found that several adult female capercaillie in the Alps actively visited more than one lek during the same season. Apparently, female preference behaviour is not fixed, and females may actively visit several leks if the number of males on the leks is small, as suggested by Storch (1997). Such conditional behaviour may also apply to formation of new leks.

Boreal forest grouse species like capercaillie have evolved in dynamic landscapes governed by forest fires (Zackrisson 1977). The natural condition has been a mosaic of different successional stages. As capercaillie males are closely associated with later successional stages in winter (Gjerde & Wegge 1989) and spring (Rolstad & Wegge 1987a,b), vacant space with no leks

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would have been common in larger areas with early successional stages after fire. Today forest fires are suppressed but have their counterparts in areas with clear-cut and young plantations. When pine forests reach the age of 25-30, they are colonised by female capercaillie, and also partly by subadult males (Gjerde & Wegge 1989). Finally, new leks will arise in the vacant area. The youngest pine forests with leks that have been reported were 45-60 years old (Winquist 1983, Valkeajärvi & Ijäs 1986, Rolstad & Wegge 1987a). The 20-year delay between female colonisation and formation of leks may be due to a low density of males, unwillingness of females to mate in too dense forest, and several years of unsuccessful attempts by males to keep females in the area until mating (see below).

The choice of a new generation

Display activity outside or in the periphery of leks has been reported in several species (Höglund & Alatalo 1995). This may be related to polymorphism as for the satellite males in the ruff *Philomachus pugnax* (Hogan-Warburg 1966), or it may be related to age or status. In capercaillie, full territorial status on leks is usually not obtained by males before they are three years old (Hjorth 1970, Wegge & Larsen 1987). Before that age the probability of mating at established leks is low. Singly, or at a lek attended only by subadult males the chances of mating would be much higher. A young male would probably benefit from a combination of two strategies: 1) obtaining a territory on an established lek and 2) trying to mate females outside the regime of dominating adult males, i.e. in newly colonised area. If he succeeds with the latter strategy, a new lek may arise.

Adult females were faithful to their nesting sites and mated on the same lek in successive years. Most of them (63%) stayed until mating in the general area occupied during winter, and then moved to a specific lek site in the vicinity (Wegge 1985, Gjerde & Wegge 1989). The others moved to leks and nest sites 2-8 km away. Yearling females choose lek site for the first time and may more easily be attached to a new lek site. However, if they stay together with adult females and copy their behaviour (Gibson & Höglund 1992), they will tend to mate at established leks. Another prerequisite for settling on an attempted lek close to their winter ranges is that natal dispersal has been completed. Data on natal dispersal are scarce, but indicate that some females disperse in their first autumn and others disperse in both autumn and spring (Rolstad 1989). The young radio-marked female at the premature lek Svarttjernet dispersed 8 km after the lek situation broke up.

In brief, the spacing of leks and sex and age groups in spring indicate that new leks are mainly founded by subadult males in vacant areas between existing leks. Due to the lek site fidelity of adult females, we hypothesise that male courting of females outside existing leks is most successful when directed towards groups of yearling females.

The model

Considerable evidence suggests that capercaillie leks are formed when subadult males visit and court females in their late winter ranges. However, territoriality of adult males around existing leks strongly restricts the area in which new leks can arise. Furthermore, courted females in most cases desert the attempted leks and thus exert a strong preference for males at established leks. Thus, we conclude that three main factors seem to determine the location of capercaillie leks, and that these factors operate at different spatial scales. First, on a larger scale, territorial behaviour of adult males prevents formation of new leks closer than 1 km from existing leks, and on average they are 2 km apart. Lek site fidelity of adult males and females combined with male territoriality, create a regular spacing system of traditional leks. Thus, in a continuous habitat landscape new leks are not formed at all, unless the traditional use of lek sites is broken by catastrophic events or by random extinction of the lek populations. Second, if there is vacancy between existing leks, premature lek situations arise when subadult (or more generally non-territorial) males visit females in late winter hotspots. Finally, on a smaller scale, a new traditional lek site is established at one of several late winter hotspots only if females accept the courting males. A new lek site will attract younger recruits, and after an initial unstable period the size of the lek will largely depend on the reproduction rate and local habitat conditions (Wegge et al. 1992).

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