SPACING OF ADULT AND SUBADULT MALE COMMON CAPERCAILLIE DURING THE BREEDING SEASON

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ABSTRACT.—The spacing behavior of 58 male Common Capercaillie (*Tetrao urogallus*) was studied at Varaldskogen in southeast Norway during 1979–1985. Birds captured at leks were equipped with radio-transmitters, and their movements were monitored throughout the year. During spring, males 4 yr old and older occupied exclusive day territories of 10.2–66.0 ha that extended radially from a center at the lek. Adult cocks used the same lek and the same territory during successive years. Among marked birds, the youngest bred at 4 yr. No difference was found in territory size between breeding and nonbreeding adult males. Territories of 3-yr-olds (60.8 ± 10.4 ha) were larger than those of older males (26.3 ± 5.0 ha) and were located farther from the lek. All territories were within a 1.2-km radius of the lek center and were maintained from early April to the end of May. Yearlings and 2-yr-old males were nonterritorial. They moved irregularly among different, neighboring leks, settling near one lek at the end of their second spring season. When associated with one lek, their home ranges were 3–6 times larger than and overlapped peripherally the territories of resident adults. Established subadult and adult males did not change territories when vacancies were created by deaths of older birds, and successful matings were not dependent on occupying a particular territory. *Received 16 December 1985, accepted 7 March 1987.*

THE Common Capercaillie (*Tetrao urogallus*) is the largest and most sexually dimorphic tetraonid species. Males are polygynous and interact with females only when they visit the lek for a few days to mate in early spring. Based on the spatial arrangements of males at the lek, where individuals are reported to occupy large contiguous or noncontiguous territorial centers of 0.1–0.8 ha (Lumsden 1961, Müller 1979, Hjorth 1985), the mating system is not considered by most authors to be true lekking. Wittenberger (1978, 1981) classified the capercaillie with the forest-dwelling grouse of North America that have dispersed territories. Oring (1982) considered the capercaillie more leklike and classified it as the only tetraonid in an intermediate group, more clustered than the ones above, but less aggregated than his third category that included the prairie grouse of North America and the Eurasian Black-Grouse (*Tetrao tetrix*). De Vos (1979) also considered the capercaillie in an intermediate type, whereas Wiley (1974) considered it a true lek-forming species.

Much of the confusion and difficulty regarding classification of mating systems stems from incomplete knowledge of the spatial and social relationships of the birds when they are not on the display grounds. On the basis of long-term behavioral studies of capercaillie in Sweden, Hjorth (1982) considered how males were spaced around the lek during the day. He noticed that each male departed from the lek in the same direction from which it had arrived and that two males never arrived from, or departed in, the same direction. From this, he suggested that males probably live solitarily in separate home ranges and that these were spaced regularly around the lek. Although no supporting data were presented, Hjorth (1982, 1985) implied further that the home ranges extend up to 2 km from the lek and were used by the males year-round. Our preliminary observations using radiotelemetry (Larsen et al. 1982, Wegge et al. 1982) supported Hjorth's general hypothesis, but suggested that it applied only to adult birds during the breeding season.

In other promiscuous North American tetraonids, adult males claim territories during the breeding season, while yearlings are nonterritorial and move about in search of unoccupied areas on which to settle (Bendell and Elliott 1966, Gullion 1967, Ellison 1973, Ballard and Robel 1974, Rippin and Boag 1974, Boag 1976, Herzog and Boag 1978, Zwickel 1980). In the Ruffed (*Bonasa umbellus*) and the Blue (*Dendragapus obscurus*) grouse, some adults also may be

nonterritorial (Lewis and Zwickel 1980, Gullion 1981, Lewis 1984). During spring, nonterritorial yearlings of Spruce (*D. canadensis*) and Blue grouse and most lek-forming species move considerably longer distances than resident adults, and lek species make temporary visits to neighboring leks (Koivisto 1965, Ballard and Robel 1974, Rippin and Boag 1974, de Vos 1983).

We report on the spring spacing pattern of Common Capercaillie males of different age and social status based on radio-tracking 58 individuals during 7 yr in southeast Norway. We discuss the mating system of this species along the continuum from clumped (leks) to dispersed polygyny and report on recruitment and age-related territoriality among males.

STUDY AREA AND METHODS

The study was conducted during 1979–1985 at Varaldskogen Field Station (60°10'N, 12°30'E) in Hedmark Co. in southeast Norway. Varaldskogen is in the middle boreal zone (Abrahamsen et al. 1977); coniferous forests of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) dominate the vegetative complex. Birch (*Betula verrocosa*) is the most common deciduous tree, and blueberry (*Vaccinium myrtillus*) and heather (*Calluna vulgaris*) dominate the ground layer on undisturbed sites.

Intensive logging and forest management have been practiced here for the last 30–40 yr. At the time of our investigation, about 36% of the study area was composed of clear-cuts and spruce and pine plantations up to 8 m in height; 43% of mature, largely undisturbed forest; and 10% of open, treeless peat bogs.

The fauna is typical of the middle boreal zone. Because of habitat deterioration and low recruitment, the population of *T. urogallus* was declining, averaging approximately 0.8 males/km² in spring in the 40-km² study area (Wegge 1983, 1984, unpubl. data).

We captured males at leks and attached radio transmitters to their backs (Brander 1968) with a nylon harness enclosed in silicon rubber to prevent feather and skin abrasion. Transmitters weighed about 100 g (2–3% of body mass), with a transmitting distance of 2–3 km and a battery life of about 700 days. The instrumentation seemed to have no adverse effects because successful matings were observed subsequently among radio-marked individuals of both sexes, and survival rates were high (Wegge 1984).

Males were aged according to beak measurements (Moss et al. 1979), using the following age-class intervals based on recaptured birds of known age in the study area. Males with beaks smaller than 23 mm were classified as yearlings (10–11 months old), males with beak depths of 23–25.5 mm were classified as 2-yr-olds (22–23 months), and males with beaks deeper than 25.5 mm were classified as adults (3-yr-old and older birds). Because a number of young males were studied in successive years, 9 known 3-yr-olds could be distinguished from others among the adult age group.

Each year during the breeding season, two or more persons were usually present every night on each of 3–6 leks to capture and observe display and breeding activity. We classified radio-equipped males as breeders or nonbreeders on the basis of observed mating performance. Any male that was observed to mate was defined as a breeding male, whether he mated many or few hens. During most years and at most leks, one male dominated the mating.

We captured and radio-marked 58 males at 6 leks during the spring seasons of 1979–1985. Several were recaptured during the summer molt and observed in successive seasons. Most telemetry work was carried out at 3 leks; one lek served as the main study population. Active leks (*n* = 23) in a larger overall study area were spaced regularly, with a mean minimum distance of approximately 2 km (Wegge and Rolstad 1986).

The locations of most radio-marked males were determined nearly every morning or late evening in the lek area. During the day their movements and locations were determined 3–7 times/week, except during the seasons of 1982–1984 when some males at two leks were tracked more intensively. Daytime locations, when birds were not on the display ground, were taken between 1000 and 2000, distributed evenly throughout the day. We observed males from 16 April until they ceased to attend leks for morning display. This varied among age groups: most adults attended the leks throughout May, whereas yearlings and most 2-yr-olds usually abandoned the leks 7–10 days earlier.

A total of 1,051 positions was recorded when males visited the leks, and 1,238 positions were recorded during daytime when they were away from the lek. Morning locations were used to study the movement of males among and on leks, whereas daytime locations were used to estimate sizes of home ranges and other measures of spacing.

We determined the position of each bird by the intersecting compass bearings from two or three elevated vantage points. Approximately 60% of all locations were triangulated to an area of 0.3 ha or less. Locations derived from two compass bearings at close distance were of similar precision. When tracking at longer distances (>500 m), such positions (19%) were less accurate. A disproportionately larger number of the lower-precision fixes were recorded on subadult males. We omitted these when making home-range comparisons.

We estimated the sizes of home ranges according to a modified version of Harvey and Barbour's (1965) "modified minimum area method." The distance be-

tween the two widest-spaced daytime positions was measured and divided in half. A line was then drawn clockwise among all successive outermost points that were spaced shorter than this half maximum distance. Positions farther away than the maximum distance were defined as excursions and were not included in the estimate of home-range size. By using a relatively large critical distance for connecting successive points, only 11 of 692 positions (1.6%) were excluded as excursions when estimating home ranges. These were distributed equally among young and older birds and thus did not introduce bias among age or social groups. Because home-range size is a function of sample size and increased to an asymptote with increasing number of locations, the sizes of home ranges could be estimated reliably only for males that were located a minimum of 25 times.

The location of home ranges in relation to the lek was expressed by coordinates. We defined the geographical center of a male's home range, henceforth termed "occupancy center," as the intersecting point of the average distance of daytime positions measured along the x and y coordinates from the lek center. We estimated occupancy centers for all males that were located a minimum of 10 times.

Values reported are means ± SE.

RESULTS

SPACING AND MOVEMENT PATTERNS

Spacing and movement patterns varied among age groups. Yearlings and 2-yr-olds showed similar behavior and were combined as subadults.

Adults.—None of 30 adult males visited more than one lek over a breeding season. Sixteen were monitored two or more consecutive years and none changed leks.

During the day adult males lived in separate home ranges within 1 km of the lek (Fig. 1). Except for 3-yr-olds, home ranges of older males were largely exclusive, with very little overlap. They are henceforth termed "territories." Spacing patterns at the main lek in 1982 and 1983 are diagramed in Fig. 1. Two unmarked males also attended this lek in 1982. One may have established a territory between males 4 and 5; it always arrived from and departed in that direction. The other unmarked bird arrived and departed in several directions and was probably a yearling or a 2-yr-old without a territory, possibly the same individual as male 7 the following year (Fig. 1, 1983).

Site fidelity was strong, and all (*n* = 23) but one adult bird (male 4) used the same territory
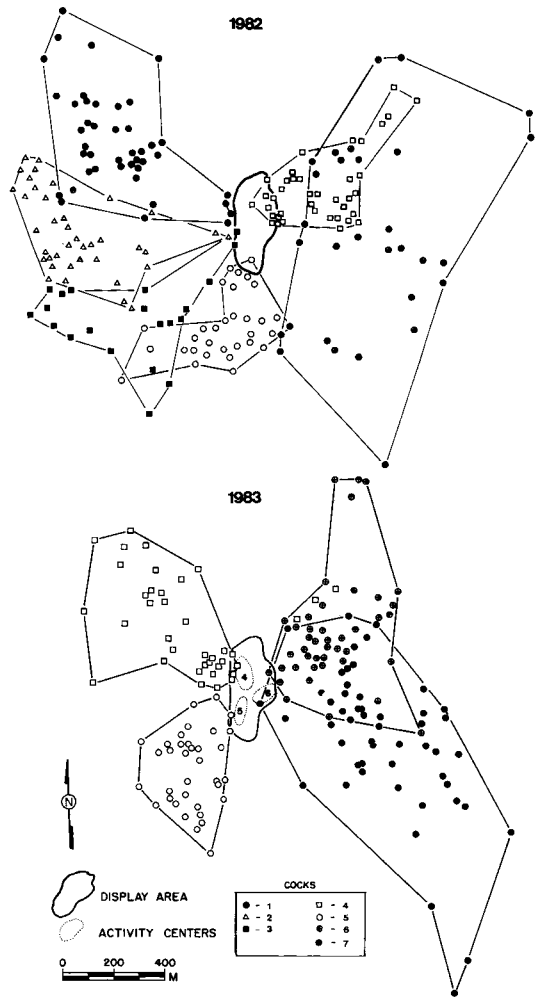

Fig. 1. Daytime home ranges of adult males attending lek C during 1982 and 1983. Males 1–3 died before spring 1983. Males 2 and 6 (1982) and male 7 (1983) were 3 yr old; the others were older. Male 1 performed nearly all matings in 1980–1982, male 6 in 1983. Activity centers on the lek are shown for 1983; male 7's is omitted because he did not establish a well-defined area of activity when attending the lek.

in successive years. During the winter of 1982–1983, males 1–3 died. Male 4 occupied his former territory during the early part of the breeding season (Fig. 1, 1983) but moved northwest and established a territory in the general former area of male 1. This was the only shift of territories recorded in eight possible instances when vacancies were created by deaths.

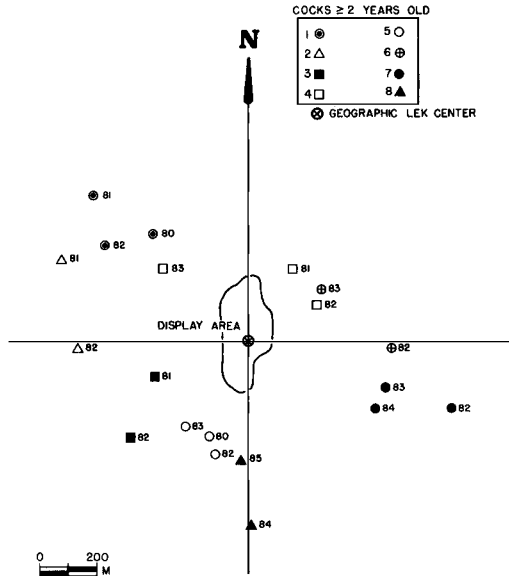Site tenacity is diagramed in Fig. 2. Occupancy centers moved a mean distance of 188 ± 22

Fig. 2. Daytime occupancy centers of males attending lek C in successive years during 1980–1985. Males 2, 6, 7, and 8 were 3 yr old in 1982, 1982, 1983, and 1984, respectively.

m between years for 12 males older than 3 yr (Table 1). Younger males seemed less sedentary. The annual change in center of home-range occupancy was larger among 3-yr-olds and youn-

ger birds than among older males (Mann-Whitney U-test, $P < 0.05$, $U = 6$, $n = 7$).

Territories of adult males varied markedly in size (Table 1). The mean size of 11 territories of 4-yr-olds and older measured 26.3 ± 5.0 ha. Territories of 3-yr-olds were larger ($\bar{x} = 60.8 ±$ 10.4 ha; Fisher-Behrens test, $P < 0.05$, $d = 2.621$). Males 6, 7, and 8 were 3 yr old in 1982, 1983, and 1984, respectively. Their territories decreased an estimated 15–40% the following year. Territories of older males did not decrease as age increased. Among 5 older males, over 9 consecutive springs, territory-size variation was much less (5–20%), and the direction of change was unrelated to age.

Territories away from leks tended to be larger than those nearer lek centers (Spearman rank correlation test, $P < 0.005$; Fig. 3). Furthermore, territories of older males were closer to lek centers than were those of younger males (Mann-Whitney U-test, $P < 0.05$, $U = 5.5$, comparison of 3-yr-olds with older males). The frequency distribution of all birds' locations measured from the lek centers also showed a clumping of older males near the lek (Fig. 4). The mean distance of all locations of 4-yr-old and older males (416 m) was significantly shorter than that of 3-yr-olds (638 m) ($t = 11.8$, $P = 0.001$, one-tailed).

During the day adults were rarely located far-

TABLE 1. Size of home range, distance of occupancy center from lek center, annual distance moved of occupancy center, and distribution of different age classes of capercaillie males at Varaldskogen, Norway, 1980–1985.

			Adult males (≥4 yr old)	
	1 and 2 yr old[a]	3 yr old	Breeding	Nonbreeding
Home-range size (ha)				
n	6	5	7	5
Mean ± SE	126 ± 36	61 ± 10	30 ± 7	21 ± 3
Range	54–246	22–79	10–66	13–36
Distance to occupancy center (m)				
n	12	7	10	11
Mean ± SE	516 ± 64	493 ± 96	364 ± 36	355 ± 42
Range	318–810	390–630	210–510	190–560
Annual change in occupancy center (m)				
n	4	4	12	
Mean ± SE	312 ± 83[b]	214 ± 52[b]	118 ± 22[c]	
Range	210–420	110–340	40–270	
Radio locations within 1 km of lek				
n	304	286	648	
Percentage of total	79	89	98	

[a] Two-year-olds and yearlings when associated with one lek.
[b] Mean distance moved in successive years.
[c] Excludes 1 male that changed territory and moved occupancy center 630 m.
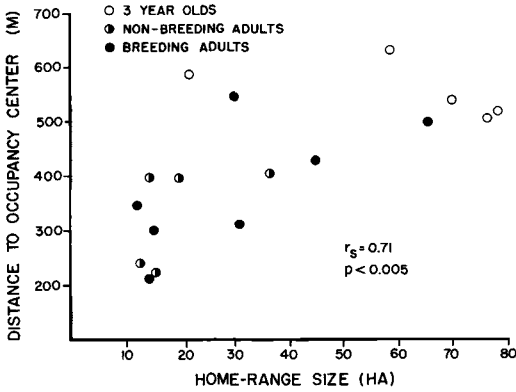
Fig. 3. Relationship of home-range size and distance to daytime occupancy centers from lek centers for 3-yr-old and older males.

ther than 1 km from the lek (Table 1). Most (95.3%) daytime locations of 3-yr-old and older males ($n = 934$) were within this radius of the lek centers.

Subadults.—In contrast to older males, yearlings and 2-yr-olds rarely established fixed home ranges or territories near one lek. Instead, they were more mobile, visiting two or more leks, and when associated with one lek their home ranges were larger than those of older, resident males (Fig. 5, Table 1). Home ranges of 2-yr-olds overlapped each other as well as the territories of adults (Fig. 5). Yearlings associated with one lek showed similar movements. The estimated home-range size of 2-yr-olds (126 ± 36 ha) probably underestimated the actual living space of this age class, because more mobile individuals could not be tracked intensively enough to generate sufficient locations for home-range estimates.
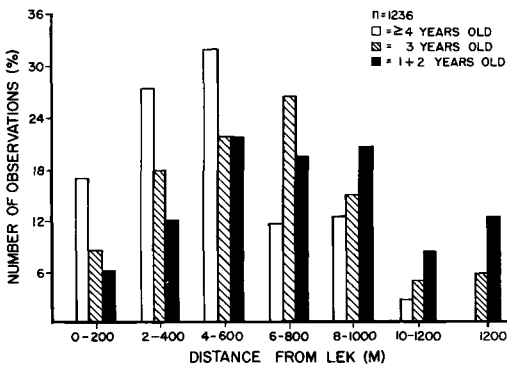

Fig. 4. The distribution of different-age males, located by radio transmitters, in relation to lek centers.
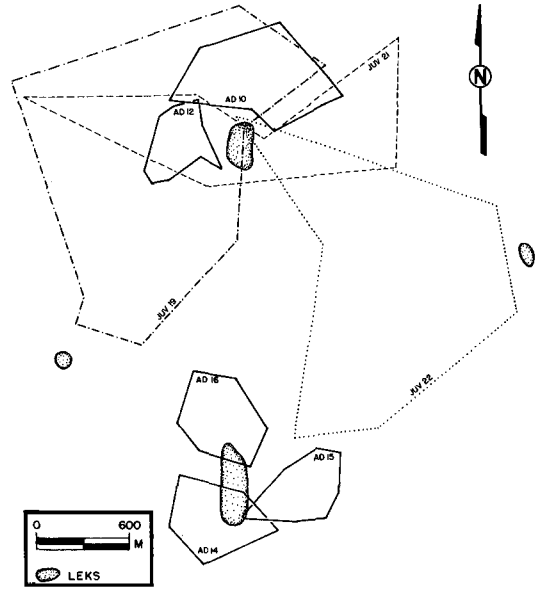

Fig. 5. Home ranges and movement pattern of 3 2-yr-old males (19, 21, 22) captured at lek A (top) in relation to leks and territories of 5 older, resident males. Only daytime positions were included when drawing boundaries. Territory sizes of males 14–16 are underestimated because each is based on fewer than 20 locations. Home ranges of males 19 and 22 are based on 19 and 11 locations, the remainder on more than 25 locations.

The extent of interlek movement varied during the season (Table 2). Before 25 April, 11 of 14 birds visited more than one lek. After 25 April, only 7 of 22 moved to another lek ($\bar{x} = 6.275$, $P = 0.012$). Because nearly all mating occurred between 25 April and 3 May (Wegge unpubl. data), interlek movement was confined mainly to the beginning of the breeding season. Reduced movement later in the season seemed to result from more stationary behavior among 2-yr-olds (Table 2). The difference was not significant ($P > 0.25$), possibly because of small sample sizes.

One yearling visited a minimum of 3 leks over 21 days. This male also showed the longest movement, 7 km, during 24 h. Three yearlings and 1 2-yr-old visited a minimum of 3 leks. The others visited only two neighboring leks. Some could have visited other leks before they were radio-marked by us, and 4 males that we lost contact with early in the season may have visited more distant leks without our knowledge.

Occupancy centers of 2-yr-olds and yearlings

TABLE 2. Numbers of subadult males visiting more than one lek during the breeding season. More than 90% of all matings were estimated to occur between 25 April and 3 May.

	Before 25 April	After 25 April
Yearlings	5 of 6	4 of 9
Two-year-olds	6 of 8	3 of 13
All subadults	11 of 14	7 of 22

were not significantly farther from lek centers than were those of 3-yr-olds (Mann-Whitney U-test, $P > 0.3$, $U = 24.5$; Table 1). Because subadults tended to move at the periphery of older males' territories, often at different sides of the lek, their occupancy centers were closer to the lek than their individual spacing distance. Thus, when comparing the mean distance of all locations from the lek between 3-yr-olds and younger males (593 and 703 m, respectively; Fig. 4), the difference was significant ($t = 2.036$, $P < 0.10$, one-tailed).

One yearling and 3 2-yr-olds changed their occupancy centers an average distance of 312 m among years. This was longer than observed in any other age group (Table 1), but because of large variation and small samples it was not significantly different from that of 3-yr-olds ($P > 0.4$). The data are not representative for subadult males in general, because more mobile birds could not be included in this comparison. Three 2-yr-olds reappeared and established territories in the same general area they had occupied during the latter part of the breeding season the previous year. Of 304 daytime locations for yearlings and 2-yr-old birds, 79% were within 1 km of the center of the lek with which they associated, and on which they later settled.

BREEDING AND RECRUITMENT

Of 17 mated males, 6 were known to be 4 yr old and 7 were at least 4 yr of age. The remaining 4 were at least 3 yr old, and probably older, according to their territorial spacing pattern near the leks. Two breeding males were a minimum of 7 yr of age.

The territories of breeding males were the same size as those of nonbreeders of equal age (Table 1; Fisher-Behrens test, $P > 0.3$, $d = 0.631$). There was no difference in the mean distance of occupancy centers from the lek (Mann-Whit-

ney U-test, $U = 16$, $n = 5$, not significant) or in the mean distance of individual locations from the lek ($t = 0.808$, $P > 0.4$, df > 500) between these two social groups.

We observed closely the changes of breeding males at leks A and C. All changes occurred following the death of the previous resident breeder. Only once, out of 9 such instances, was the vacant territory of the former breeding male (male 1) taken over by a neighbor (male 4; Figs. 1 and 2). That change did not result in matings. Another younger bird (male 6, age 4 yr) achieved mating status instead. During 7 yr of observation at lek C, 95% or more of all matings were performed by 6 males. Thus, nearly all territories around the lek were occupied one year or another by a breeding male. We observed a similar "rotation" of breeding territories at lek A.

None of 7 3-yr-olds was seen to mate. They rarely established well-defined activity centers within the lek area, and their home ranges were usually larger than and peripheral to the territories of older males. When vacant space was created by the death of an older bird, a new 3- or 4-yr-old did not invade. Instead, they reoccupied the home range from the previous spring, concentrating in the area closest to the lek center. This pattern occurred in males 6–8 (Figs. 1 and 2), which we followed during their recruitment period until they became breeding males at the age of 4 yr in 1983, 1984, and 1985, respectively.

DISCUSSION

Daytime home ranges of adult males were largely exclusive. When establishing themselves around a lek, 3-yr-olds usually settled between the home ranges of older, resident birds. Although their home ranges overlapped those of older males to some extent, this overlap occurred mainly during the first part of the breeding season. Later in the season 3-yr-olds were separated spatially and temporally from other adults. Thus, spring home ranges of adult Common Capercaillie males may properly be termed territories, after the definitions of Pitelka (1959) and Davies (1978).

After the breeding season, territories were abandoned and males were dispersed with respect to the location of leks and conspecifics (Larsen et al. 1982, Wegge et al. 1982, unpubl. data). Furthermore, during spring males did not

venture farther than 1 km from the lek. Thus, the spacing pattern envisioned by Hjorth (1982) applies only to older, resident birds during April and May within a small area adjacent to the lek. Designating the area adjoining a lek as a "recruiting area" (Hjorth 1985) is also misleading because young birds (yearlings and 2-yr-olds) were nonterritorial and moved over larger areas (often across leks) before settling. Young males in areas next to a lek during winter were not necessarily recruited to that lek population.

The spacing pattern, 20–30-ha territories surrounding a central lek area with clustered, usually contiguous activity centers of less than 0.5 ha, shows that males are highly clumped at the time of mating. The spacing resembles true leks more than that of dispersed males found among North American forest grouse. Although the territories of Ruffed and Spruce grouse also seem to be spatially clumped (Gullion 1967, Boag 1976, Herzog and Boag 1978), possibly because of habitat (Gullion 1976), the males of North American forest grouse display solitarily within their territories. They do not normally form communal displays, as seen in capercaillie.

Hjorth (1982) was the first to point out that capercaillie males probably have separate spring home ranges and that leks are located at the apices or the intersecting point of these ranges. Our results confirm this. The lek area was not part of the daytime territory of any of the males. They visited it only for display and other activities related to mating. In this respect the system also resembles that of true lekking grouse with collective displays, where individuals claim small, exclusive territories but the arena or lekking ground belongs to nobody (Hjorth 1970, de Vos 1979).

Polygynous grouse with dispersed territories (e.g. forest grouse in North America) establish permanent territories in which they live continually during the breeding season. Grouse displaying at communal leks (e.g. Eurasian Black-Grouse and open-dwelling tetraonids in North America) are territorial only when on the lek (Robel 1969, 1970; Wiley 1973; Rippin and Boag 1974; de Vos 1979). In this respect, the Common Capercaillie conforms to the pattern of other forest-dwelling species with dispersed territoriality.

The mating success of capercaillie was not related to occupation of any particular territory, and no difference was noted in territory size between successful breeders and nonbreeding adult males. Because hens move independently of males and their daytime territories when visiting the leks for mating (Wegge 1985), the size or quality of a male's territory has no value for hens. Thus, increasing the territory size to intercept hens moving to the lek does not improve the breeding fitness of a male. Increases in the daytime territory will reduce the number of competitors at the lek. In forested habitats, territory defense probably consumes more time and energy than in open terrain where visual and acoustical communications are transmitted more easily. Beyond a point, territory acquisition and defensive behavior may be too costly in terms of exposure to predators and of reduced physical fitness for performing at the lek.

Capercaillie are highly aggressive during the mating season (Hjorth 1970, 1982; Moss 1980; Jones 1981). A random distribution of males around the lek would lead to frequent encounters and trigger aggressive behavior during daytime. Pirkola and Koivisto (1970), for instance, reported that flight or sound from other individuals elicits display activity outside the lek during the day. In forested habitats, trees and topographic features provide cover that reduces visual and auditory contact between neighbors. Thus, in denser habitats males may be spaced closer together without mutual interference. This may explain why territories are smaller when they contain a larger proportion of older trees (Larsen and Wegge 1985, Wegge and Rolstad 1986).

Small territories were located nearer the lek than were larger territories (Fig. 3). Close proximity to the lek probably facilitates detection of sporadically visiting females (Bradbury 1981), especially those returning to the lek for remating. Thus, we argue that males establish day territories as close as possible to the lek, but sufficiently far away to avoid daytime intermale interference. In Common Capercaillie such daytime territories may serve for rest and energy conservation, and may have evolved by giving a selective advantage at the mating ground to individuals adopting such off-lek behavior.

Adult males did not change territories when vacancies occurred, and settled 2- and 3-yr-olds did not take over vacant territories when available in the next season. Instead, once a male settled at a lek, he remained in the first general area of occupancy, gradually constricting his

territory nearer to the lek. Strong site fidelity, as in the three North American forest grouse (Blue Grouse, Bendell and Elliott 1966; Ruffed Grouse, Boag 1976; Spruce Grouse, Herzog and Boag 1978), may be advantageous to long-lived, forest-dwelling species. Experience on a territory may compensate for any quality differences between territories, especially because territories seem to have no resource attraction for females (Wegge 1985, unpubl. data).

Following 1 or 2 yr of nonterritorial, interlek movements, males settled at one lek and established life-long territories. The nonterritorial subadults were not "surplus" birds, as suggested for the smaller, monogamous Willow Ptarmigan (*Lagopus lagopus scoticus;* Watson and Moss 1980). They were more like "standby birds" (Zwickel 1980), and constitute an important part of the breeding population (Jamieson and Zwickel 1983). Because of poor breeding success for several years (Storaas and Wegge 1985), the density of males at most of our leks was estimated to be below any equilibrium level theoretically set by available territorial space. Vacancies were also created each year through deaths of older males. Yearlings and 2-yr-olds did not settle quickly on these territories. Instead, they continued their extensive movements among neighboring leks.

The existence of nonterritorial birds in the presence of available territories has been reported in Blue Grouse (Lewis and Zwickel 1982, Lewis 1984) and in Ruffed Grouse (Gullion 1981). Recruitment therefore may depend on factors other than the availability of space. Such behavior has been cited as evidence of delayed breeding (Lewis and Zwickel 1982, Jamieson 1985), thus supporting Wiley's (1974, 1981) general hypothesis of adaptive bimaturism. For Common Capercaillie, we question such an interpretation on the grounds that yearlings and 2-yr-olds participate actively (and the latter aggressively) in the social interactions at the lek (Hjorth 1982, pers. obs.). Further, unlike species in other taxa with delayed breeding, yearling capercaillie males have the conspicuous, dark plumage of adults. Finally, yearlings are physiologically able to breed (Berger and Aschenbrenner pers. comm.) and have been reported to court females (Jones 1981). We observed once a yearling male attempting to copulate with a stuffed hen on a lek. Instead of delaying breeding, subadult capercaillie males probably fail to breed because they cannot compete effectively for territories, an interpretation consistent with Wittenberger's (1981) for lekking grouse in general.

Nonterritorial behavior and interlek movements by the two youngest age classes were not caused by a high density of resident males, because they occurred when territories were available. If territorial behavior regulates breeding numbers in capercaillie, it probably occurs at higher densities than in our study area. From the observed spacing pattern, we predict that such territorial regulation affects the establishment of 3-yr-olds rather than of younger birds.

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The **XX International Ornithological Congress** will be held **2–9 October 1990** in **Christchurch, New Zealand.** Professor Charles G. Sibley (USA) is President, and Dr. Ben D. Bell (NZ) is Secretary-General. The anticipated Congress program will include plenary lectures, symposia, contributed papers (spoken and posters), workshops, discussion groups, and films. There will be a mid-Congress excursion. Pre- and post-Congress excursions are planned to interesting ornithological sites in New Zealand and adjacent regions. Requests for the First Circular and suggestions regarding Congress organization should be addressed to **Dr. Ben D. Bell, Secretary-General, XX International Ornithological Congress, Department of Zoology, Victoria University, Private Bag, Wellington, New Zealand.**