Are female Black Grouse *Tetrao tetrix* territorial?

P. K. Angelstam, M. Jaarola & N.-E. Nordh

Angelstam, P. K., Jaarola, M. & Nordh, N.-E. 1985: *Are female Black Grouse* Tetrao tetrix *territorial*? — Ornis Fennica 62:124–129.

The hypothesis that female Black Grouse actively space out areas and defend them from conspecific females during the breeding season was tested by examining the daily and seasonal distribution of the cackle-call, by territory mapping using the call, by studying seasonal variation in group formation and by play-back experiments.

Females started to cackle about one week before the mating period and stopped in the beginning of the incubation period. The cackle-call was heard only during a 3-h period around sunrise. The observations suggested that the cackle-call is used in agonistic interactions between females, but the results of play-back experiments were not conclusive.

Territory mapping based on the total cackle records gave a density estimate which closely coincided with other independent estimates.

Altogether, the results did not contradict the hypothesis tested.

P.-K. Angelstam, M. Jaarola & N.-E. Nordh, Grimsö Wildlife Research Station, S-77031 Riddarhyttan, and Department of Zoology, Section of Animal Ecology, Box 561, S-75122 Uppsala, Sweden

Introduction

In polygynous tetraonid species in which males do not take part in the care of the young, the males have advanced social systems with elaborate display behaviour and strong territoriality (Johnsgard 1983). Recent studies of some polygynous tetraonid species in North America – the Spruce Grouse *Canachites canadensis franklinii* (Herzog & Boag 1977, 1978, Nugent & Boag 1982) and the Blue Grouse *Dendragapus obscurus* (Hannon 1980, Lewis 1984, Bergerud & Butler in press) — report that the females also have territories, which they defend by aggressive behaviour and calls. In general, the territorial systems of males and females appear to be separate (Nugent & Boag 1982, Hannon 1980, Lewis 1984, Bergerud & Butler in press).

In Fennoscandia there are two exclusively polygynous grouse species: the Black Grouse *Tetrao tetrix* and the Capercaillie *Tetrao urogallus*. There are indications that the females of these species may show territoriality during the breeding season. Firstly, in both species the home-ranges of the females during egg-laying and incubation are spaced out (Angelstam unpubl., Wegge in press, respectively). Secondly, during the mating season the females of both species have a loud, far-reaching nasal cackle-call, the function of which is unknown (Selous 1909–1910, Koivisto 1965, Boback & Müller-Schwarze 1968, Glutz et al. 1973).

In this study we tested the hypothesis that Black Grouse females are territorial during the breeding season by examining the seasonal distribution of cackle-calls, by play-back experiments and by attempting territory mapping using the cackle-call.

Study area

The field work was conducted from early April to late May in 1984 within the Grimsö Wildlife Research Area (59°40'N, 15°25'E), in south-central Sweden. The study area is a flat mosaic of open and forested raised bogs, interspersed with even-aged blocks of young (5–15 years) and mature (>100 years) forest stands (Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*) at an altitude of 100 m. For a detailed description of the Grimsö area, see Angelstam et al. (1982).

The density of Black Grouse males in this part (SE) of the Grimsö Research Area in spring 1984 was estimated at 2.3/km^2 (Angelstam unpubl.).

Methods

Daily and seasonal distribution of cackle-calls. Observations were made in the morning and evening along a fixed route of about 6 km to study the daily and seasonal distribution of spontaneous cackle-calls of Black Grouse females outside the arenas. The route ran along woodland roads and the marginal fens of raised bogs. At 15 stations, situated at 300–600 m intervals along the route, a 3-minute stop was made to listen for vocalizations. In addition all vocalizations between stops were noted.

Cackle-calls of Black Grouse females may be heard at a distance of 1 km in open terrain (Boback & Müller-Schwarze 1968). If we assume that cackle-calls may be detected with certainty at half that distance, our auditory observations covered an area of 4.0 km^2 (excluding 0.5 km^2 open wet fen/bog).

For each female vocalization the following was noted: duration, time, location and, when possible, behaviour of observed females and males. The location of lekking and solitary displaying males was also noted. The intensity of calls was classified in three categories: 1 — one series, 2 — two series and 3 — more than two series of cackles. Cackle-calls from arenas were excluded. The walking direction was alternated and the starting station varied from day to day.

Listening was initiated 1.5–1 h before sunrise and terminated 2–2.5 h later. A total of 20 censuses were made: one on 21 March, 17 censuses spaced regularly between 12 April and 13 May, one on 23 and one on 30 May. The three first cencuses were made on skis.

Another period of high Black Grouse activity occurs in the evening (Hjorth 1970). Therefore listening was also carried out every second evening from 1 to 7 May, starting 1.5–0.5 h before sunset and concluding 2–2.5 h later.

Is the cackle-call an aggressive call? To test whether Black Grouse females respond to cackle-calls of other invidivuals, two types of play-back experiments were performed. (Cackle-calls of female Black Grouse were recorded within the study area on 26 April when females were provoked with a cackle-call recorded at a lek by S. Palmér 1963. A Uher 4400 Report Stereo IC recorder at 19 cm/s and a parabolic reflector were used).

For the first experiment the cackle was copied on a casette as follows: one minute cackle — one minute pause, repeated three times. As control calls we used the cackle of a Capercaillie female *Tetrao urogallus* — a locally sympatric polygynous grouse species — and the call of the Cuckoo *Cuculus canorus* — a call of equal audibility and common in the study area. These calls were copied in a similar way. The tape was played at the route stations, one species' call at each station, each species' call at every third station. Different calls were played at the same station on consecutive playbacks. Notes on behaviour were made as previously described. These experiments were made regularly from 27 April to 11 May, at least twice a week. The experiments began 1–0.5 h before sunrise and terminated 3–3.5 h later.

For the second experiment three sequences of the recorded cackle were copied on a one-minute endless tape. Two individually known females, carrying radio-transmitters (see Brander 1968, Angelstam 1983, 1984 for details), were then provoked with the call.

The females were located using a four-element hand-antenna and approached to within 200 m distance (estimated from triangulation and the signal strength of the transmitter). Then a stuffed Black Grouse female mounted on a 2-m-high pole was put up in an open place. A tape-recorder with the endless cackle-call tape was placed close to the stuffed female; it was started and the observer withdrew to a hiding-place roughly 100 m away. The behaviour and vocal responses of the two females and males in the vicinity of the dummy were noted. The tape was played for 15-65 minutes (mean 40 minutes) starting at sunrise. The experiment was carried out on five mornings between 3 and 11 May, each morning in two different but adjacent places.

Hens were also provoked with cackle-calls during incubation. The nests of the radio-marked females were found by tracking the incubating females and the breeding chronology was estimated from the egg weight loss (see Angelstam 1984). On 28 and 29 May play-back was performed about 100 m from the incubating hens. For each female the cackle was played for 15+10 minutes, 30 and 90 minutes after sunrise.

Territorial mapping. In an attempt to map the territories of the female Black Grouse in the study area, all cackle calls heard during visits to the area were used. The results were evaluated according to the territory mapping method described in Anonymous (1978) and by Svensson (1978). Special attention was paid to simultaneous observations of cackling females.

Group size. The seasonal variation in group size of Black Grouse females was estimated from: 1) Weekly observations within the Grimsö Research Area (carried out by the personnel at Grimsö Research Station) from September 1978 to May 1984. Observations from arenas were excluded. 2) Observations of flushed radio-equipped Black Grouse females during 1977–1981.

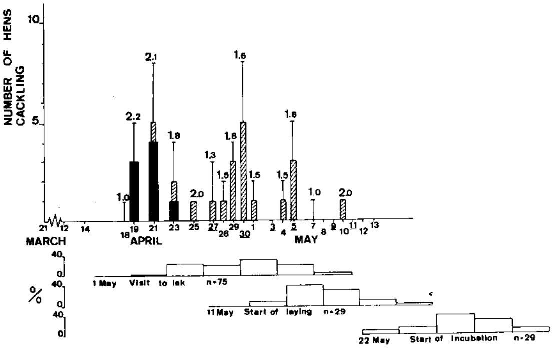

Fig. 1. Seasonal distribution of the cackle-call of female Black Grouse during the breeding season. The intensity of the cackle-call is graded from one series at a time (thin bar) to several series at a time (dark broad bar), the number being given above each bar. Data on the breeding phenology of Black Grouse females (in this study area) from Angelstam (1984). Underlined dates denote when playback tests were made.

Results

Seasonal and daily distribution of cackle-calls. The 20 censuses from 21 March to 31 May yielded a total of 30 cackle-calls, heard between 18 April and 10 May (Fig. 1). The additional 17 cackle-calls heard in association with play-back experiments were confined to the same period. There was no difference in the seasonal distribution of the two groups of calls. Both the temporal distribution and the intensity of the cackle-calls showed a marked peak in the beginning of the breeding season. Fig. 2 shows the daily distribution of cackle-calls. The total cackle period was almost three hours. No cackles were heard during the listening time in the evening.

Using triangulation it was shown that cackle-calls could be located from a distance of about 500-600 m. This supports the assumption used in calculating the area covered by the auditory observations.

Is the cackle-call an aggressive call? Black Grouse cackle-calls were heard on four of the six play-back routes (Fig. 1). Of the total of 17 Black Grouse cackles, eight were heard after playing Black Grouse cackle, two after Capercaillie cackle, four after the Cuckoo call and three before playing any call. There was no significant difference in the female Black Grouse response to the three different calls ($0.10<P<0.20$, $\chi^2=3.99$). On four occasions cackles of Capercaillie were heard only after playing Capercaillie cackle.

Black Grouse males, both solitary and lekking, often responded to the cackle-call by starting or intensifying the display and, on a few occasions, by approaching the female cackle.

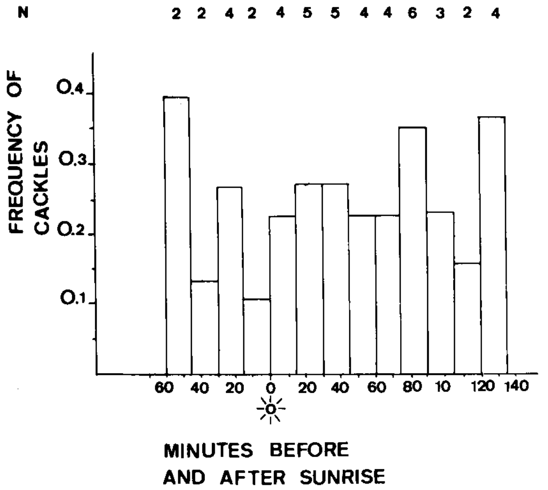

Fig. 2. Daily distribution of cackle-calls. The frequency is expressed as the total number of cackles per 15-minute period.

In the 10 play-back tests with the radio-marked females, cackles were heard on one occasion (see case 5 below). There was no attack upon the dummy; the females were not seen during the experiments but for most of the time they remained within 200 m of the observer. On a few occasions the females approached the tape-recorder and a few times were so close that they were heard flying. In a natural situation a female was observed chasing another female, both of them giving cackle-calls (see case 1 below) and answering each other's cackle. The following case histories describe the observations in greater detail.

Case 1; 19 April, 06.50

A series of 7–10 "ca" s was repeated three to four times by a female (A) sitting in the forest NE of a small lake. Thereafter a female (A or B) flew from the NE, continuously cackling, toward the S. She was immediately joined by a male, which had been sitting on a nearby bog.

Another female (B or A), cackling intensely, followed about 200 m behind. When the other birds disappeared, she turned off N, still cackling.

Case 2; 21 April, 05.21–05.26

A female (A) was flushed at 05.21 from the marginal fen of a bog. She flew, cackling intensely, 250 m across the bog, where another female (B) immediately started to cackle. Then female A moved away from female B, while female B continued to cackle until 05.26.

Case 3; 28 April, ca. 05.30

After three (A, B and C) stationary females ca. 200 m apart had been heard cackling for about 10 minutes, B suddenly flew to C and both females started to cackle very hard, using a 3-syllable call, "ca-ca-caa", during 3 minutes. Thereafter one of them (B?) flew back and the same spacing of the three females was restored. All females then became quiet.

Case 4; Play-back experiment, 28 April, 04.20–05.10

When the endless cackle-call tape was played, one female responded repeatedly, uttering the 3-syllable call. She also walked towards the tape-recorder from a distance of 250 m to 100 m. When the tape was stopped, the female became quiet within one minute. When the tape was started again, the female responded within ca. 10 seconds with continuous cackling. This sequence of events was repeated three times during the 50 minutes.

Case 5; Play-back experiment, 5 May, 05.00–06.00

After 15 minutes female no. 36 started cackling (several series repeated about every second minute) and continued to do so for 12 minutes, whereafter she flew to a group of trees (S) closer to the dummy than the previous location. She then cackled more intensively (longer series) for 5 minutes, after which she flew further away (N), remaining silent.

Fifteen minutes later female no. 37 approached the stuffed female, and sitting in a tree 150–200 m away she cackled for 5 minutes. The cackle was more intensive than that of 36, and each series of cackles ended with a pronounced "caa". Female 37 remained in this part of the study area, but 36 flew away and was never found here again.

A male was sitting on a nearby bog during the experiment, hissing when the females cackled, otherwise mostly silent.

The females did not respond to play-back during incubation.

Territory mapping. Eleven probable territories were found (Fig. 3), which means a minimum density of 2.8 females/km^2 within the mapped area. Another female may have been resident in the northern part of the area (Fig. 3). This would give a maximum density of 3.0 females/km^2.

Two of the territories found during the territory mapping coincided reasonably well with the home-ranges of the two radio-marked females (nos. 37 and 38) resident in the study area (see Fig. 3).

Group size. The groups of Black Grouse females were largest in early winter and then decreased, so that the females were almost always (90 times out of 93) observed alone when the egg-laying started in early May (Fig. 4). The females remained single until the beginning of July, i.e. 2–4 weeks after hatching.

Discussion

The cackle-call was confined to a short period during the breeding season and ended just before the start of egg-laying. The play-back experiments failed to produce any evidence of territorial defence, but other circumstantial observations suggested that the hens may have a behavioural system leading to spacing out of the home-ranges during the breeding season.

Function of the cackle-call. Two categories of territorial defence are described by Brown & Orians (1970): 1) "actual defence, such as attacking, chasing and threatening rival intruders...", 2) "identifying acts" such as certain calls and displays.

Identifying acts must keep rivals out in order to be designated as territorial signals (Brown & Orians 1970) i.e. territory owners should respond to calls of intruders. For example Hannon (1980) found that female Blue Grouse responded to cackle-calls and sang duets in the wild. Nugent & Boag (1982) observed that female Spruce Grouse advertised and probably maintained territories by a call similar to the cackle of Blue Grouse females.

Aggressive behaviour among Black Grouse females at arenas has been described by several authors (e.g. Selous 1909–1910, Kruijt & Hogan 1967, Hjorth 1970). "With carpals somewhat lowered, tail spread out, giving "isch"-calls one female chases another, which usually retreats (Koivisto 1965: Fig. 5)". Following Conder (1949), Koivisto (1965) suggested that this might be used in maintaining an individual distance.

Play-back experiments with the cackle-call evoked no aggressive behaviour in Black Grouse females. Either they do not respond in this way or the number of tests was too small and/or the timing of the tests too late.

However, the hypothesis concerning the function of the cackle-call is supported by other observations: Firstly, females can be provoked to answer the cackle-call (see case 4). Secondly, vocal contests were observed (cases 2, 3 and 5). The course of events in case 5 can be interpreted in two ways. Either the females responded to the taped cackle or were cackling at each other; but both interpretations suggest that the females were answering the cackle of another hen.

Herzog & Boag (1977) and Nugent & Boag (1982) observed agonistic interactions between female Spruce Grouse: females chasing each other, giving aggressive calls. Hannon (1983) provoked territorial female Willow Ptarmigan with a dummy, inducing attacks from half of the females. The most aggressive behaviour among grouse females has been described by Bergerud & Butler (in press) for Blue Grouse. Using a taped cackle-call and a female dummy they provoked fierce attacks on the dummy. Some of the females "...continued attack until snared".

One case of actual defence was observed (case 1), but no physical interactions. Koivisto (1965) once observed a Black Grouse female chasing another, one of the females cackling. Koivisto (1965) also noted that the cackle cannot always be connected with aggression. It may be that the cackle-call is adapted to what Eibl-Eiblesfeldt (1975) describes as "actual vocal battles that prevent more bloody encounter". It may be noted, however, that the Black Grouse is very elusive compared with North American grouse species. It is obvious that the territorial behaviour of Black Grouse females is not as intense as that of females of the North American grouse species described above.

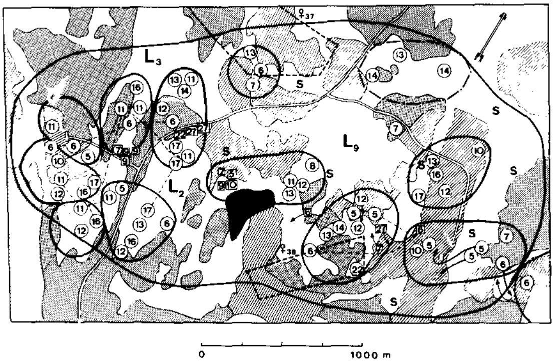

Fig. 3. Map of the area (within large thick circle) where territorial mapping was attempted. The figures denote the date (cf. Fig. 1) on which an observation was made. Small thin circles denote cackling females, squares observed but silent females, arrows flight direction, and dashed lines simultaneous observations. Individual "territories" are marked with small thick circles. Broken-line polygons denote home-ranges of the two radio-marked females. L_x = lek with x males, S = solitary displaying males, hatched areas = mature forest, dotted areas = young forest, white areas = bog, dark area = lake.

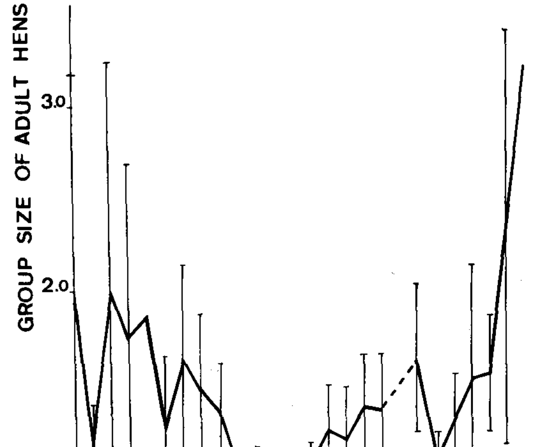

Fig. 4. Seasonal variation in size of groups of adult females in relation to breeding phenology and cackle period. Vertical lines denote 95 % confidence limits. The confidence limits for the last mean group size of the year have been omitted from the figure because of their large size on this scale (± 4.41).

Most of the cackles heard were uttered by single females without any male displaying in the immediate vicinity and without any female answering. This may indicate that the cackle-call is used as a repelling vocalization, probably given spontaneously, which suggests that females may achieve spatial separation by mutual avoidance (Tinbergen 1957) and not just by actual combat and overt defence of territories. Studies on the function of the female territory calls of other polygynous grouse species confirm Tinbergen's hypothesis (Herzog & Boag 1978, Nugent & Boag 1982, Hannon 1983, Bergerud & Butler in press).

As the cackle-call is very variable, individual differences (cf. Nugent & Boag 1982) are probably sufficient to be used as assessment cues (Dawkins & Krebs 1978).

The seasonal distribution of cackle-calls also supports the hypothesis that the cackle is used in establishment of nesting territories. The Black Grouse females started to cackle about three weeks before the beginning of incubation and stopped when incubation began (Fig. 1). The last cackle was heard one day before the mean date of the start of egg-laying (11 May). Moreover, the females seemed to be more mobile and the cackling was most intense in the beginning of the cackle period (Fig. 1), i.e. at the time when the establishment of territories probably takes place.

Why did the seasonal cackle period end at the beginning of incubation? The seasonal pattern of mortality among Black Grouse females suggests that the briefness of the cackle period is an adaptation to minimize conspicuousness for predators, although this would mean reduction of territorial advertisement and defence. Before egg-laying has started the mortality rate is very low, but with the onset of egg-laying, when nutritional and energetic needs put a strain on the females, the mortality rate rises drastically (Angelstam 1984). A similar decline of aggressive calls with the onset of incubation has been reported for Spruce Grouse (Alway & Boag 1979, Nugent & Boag 1982) and Blue Grouse (Stirling & Bendell 1970, Hannon 1978).

Some of the results suggest an alternative, or additional, function of the cackle-call. The seasonal cackle period concurs with the mating period (Fig. 1) and the daily cackle period (Fig. 2) coincides with the females' daily arena visit (Kruijt & Hogan 1967). Thus, the cackle may also serve to synchronize and stimulate the sexual behaviour of males and females, as suggested for Blue Grouse (Stirling & Bendell 1970) and Spruce Grouse (Nugent & Boag 1982). (Note that these species do not lek, so that a mating call is probably more functional than it would be for Black Grouse.) Observations of females cackling at arenas (e.g. Selous 1909–10, Koivisto 1965, Boback & Müller-Schwarze 1968, own obs.) also support the mating-call hypothesis.

The cackle-call evidently stimulates and attracts males but we have not observed solitary displaying males in the immediate vicinity of cackling females, which suggests that the cackle is not directed at the males, but that it has a secondary effect due to males associating the cackle with a female.

As we have not tested the mating-call hypothesis, we cannot reject it, but we do not consider it to be the only function of the cackle-call for the reasons discussed above. Hence the cackle-call of female Black Grouse may have an intra- as well as an intersexual function.

Territoriality. Most of the territory definitions include both a "defended area" (Noble 1939) and an "exclusive area" (Schoener 1968).

Our results suggest that Black Grouse females occupy a defended area during the breeding season, as we have observed intraspecific agonistic behaviour, in which the cackle-call was used as an identifying territorial act and as an aggressive call in actual defence.

We have not been able to test whether females occupy exclusive areas, as this would require all females in the study area to be marked. The only indication of exclusiveness is that females initiate a solitary existence in this period; the final break-up of groups concurs with the cackle period (also reported by Kruijt et al. 1972).

How accurate is the density estimate of female Black Grouse based on territory mapping? An independent way of estimating the number of females within the study area is to use the pre-breeding sex ratio and the density of males. If the sex ratio is taken as 58 % females (Angelstam 1984), the density of males in this part of the Grimsö Research Area yields a female density of 3.2 females/km^2. Another, more tentative, estimate may be derived from the home-range size of Black Grouse females during egg-laying and incubation. Angelstam (unpubl.) estimated the size of such home-ranges in this study area at 32±2 SE ha (N=49). If the home-ranges are assumed to be hexagonally packed without overlap, this yields a density of 3.1 home-ranges per km^2. These estimates correspond to 13 and 12 territories, respectively, in the mapped part of the study area. The attempt to map the territories of Black Grouse females resulted in 11 or 12 clusters. The similarity of these estimates suggests that, although time-consuming, territory mapping with the aid of the cackle-call may be used as a method of censusing female Black Grouse.

To summarize, we cannot reject the idea that female Black Grouse have a social system leading to spacing out of home-ranges during the breeding season. Aggressive behaviour is probably not the only way in which to achieve this, but avoidance (Waser & Wiley 1980) may also be an important factor. The far-reaching cackle-call is an appropriate signal for both.

Acknowledgements. We thank H. Lindén, S.G. Nilsson, J. Tiainen and S. Ulfstrand for valuable comments on earlier versions of the manuscript. Financial support was obtained from a private foundation.

Selostus: **Ovatko teerinaaraat territoriaalisia?**

Tutkimuksessa on testatttu hypoteesia, jonka mukaan naarasteeret pesimäaikana puolustaisivat aktiivisesti reviirejä muita teerinaaraita vastaan. Aikaisemmin on havaittu, että teerinaaraiden elinpiirit muninta- ja haudonta-aikana eivät ole päällekkäisiä. Lisäksi naarailla on vain lisääntymisaikana kuultava, kantava, nenäsointinen kotkotus, jonka merkitys on tuntematon.

Naaraat aloittivat kotkotuksensa noin viikkoa ennen parittelujan alkua, ja se loppui haudontavaiheen alussa (kuva 1). Kotkotusta kuultiin päivittäin noin kolmen tunnin aikana auringonnousun molemmin puolin (kuva 2). Useat havainnot vahvistivat käsitystä, että kotkotusta käytettäisiin antagonistisen, uhkailevan ja hajauttavan käyttäytymisen yhteydessä eri naaraiden välillä. Ääniatrappikokeiden tulokset olivat kuitenkin jonkin verran ristiriitaiset.

Naaraiden reviirejä kartoitettiin kotkotuksesta tehtyjen havaintojen avulla, ja kartoituksen antamat tiheysarvot olivat hyvin samanlaiset kuin muilla menetelmillä todetut tiheydet (kuva 3). Tutkimuksen mukaan on mahdollista, että teerinaaraiden ryhmäsosiaalisuus murtuu pesimäkauden alkaessa (vrt. kuva 4), mikä johtaa hajallaan oleviin, eipäällekkäisiin pesimäaikaisiin elinpiireihin. Päällekkäisyyden välttäminen tapahtunee sekä aggressiivisen käyttäytymisen että keskinäisen välttelyn kautta. Kotkotus toiminee signaalina kummassakin tapauksessa.

References

Alway, J. H. & Boag, P. A. 1979: Behaviour of captive Spruce Grouse at the time when broods break up and juveniles disperse. — Can. J. Zool. 57:1311–1317.

Angelstam, P. 1983: Population dynamics of tetraonids, especially the Black Grouse (Tetrao tetrix L.) in boreal forests. — Unpubl. Dr. thesis, Univ. Uppsala.

Angelstam, P. 1984: Sexual and seasonal differences in mortality of the Black grouse Tetrao tetrix in boreal Sweden. — Ornis Scand. 15:123–134.

Angelstam, P., Lindström, E. & Widen, P. 1982: Cyclic shifting of predation and other interrelationships in a south taiga small game community. — Trans. Intern. Congr. Game Biol. 14:53–60.

Anonynous 1978: BIN. Biologiska inventeringsnormer. Fåglar. — Statens naturvårdsverk, Stockholm.

Bergerud, A. T. & Butler, H. E.: Aggressive and spacing behaviour of female Blue Grouse. — Auk (in press).

Boback, A. W. & Müller-Schwarze, D. 1968: Das Birkhuhn. — Die Neue Brehm-Bücherei. A. Ziemsen Verlag, Wittenberg Lutherstadt.

Brander, R. B. 1968: A radio package for game birds. — J. Wildl. Manage. 32:630–632.

Brown, J. L. & Orians, G. H. 1970: Spacing patterns in mobile animals. — Ann. Rev. Ecol. Syst. 1:239–262.

Conder, P. J. 1949: Individual distance. — Ibis 91:649–655.

Dawkins, R. & Krebs, J. R. 1978: Animal signals: information or manipulation. — *In* Krebs, J.R. & Davies, N.B. (eds.): Behavioural ecology: an evolutionary approach: pp. 282–309. Blackwell Scientific Publications, Oxford.

Eibl-Eiblesfeldt, I. 1975: Ethology — the biology of behaviour. — Holt, Rinehart and Winston, Inc., New York.

Glutz von Blotzheim, U. N., Bauer, K. M. & Bezzel, E. 1973: Handbuch der Vögel Mitteleuropas. Band 5, Galliformes und Gruiformes. — Akademische Verlagsgesellschaft, Frankfurt am Main.

Hannon, S. J. 1978: The reproductive cycle, movements, and pre-nesting behavior of adult and yearling females in a population of Blue Grouse. — M.Sc. thesis, Univ. Alberta, Edmonton.

Hannon, S. J. 1980: The cackle-call of female Blue Grouse: does it have a mating or aggressive function? — Auk 97:404–407.

Hannon, S. 1983: Spacing and breeding density of Willow Ptarmigan in response to an experimental alteration of sex ratio. — J. Anim. Ecol. 52:807–820.

Herzog, P. W. & Boag, D. A. 1977: Seasonal changes in aggressive behavior of female Spruce Grouse. — Can. J. Zool. 55:1734–1739.

Herzog, P. W. & Boag, D. A. 1978: Dispersion and mobility in a local population of Spruce Grouse. — J. Wildl. Manage. 42:853–865.

Hjorth, I. 1970: Reproductive behaviour in Tetraonidae with special reference to males. — Viltrevy 7:183–596.

Johnsgard, P. A. 1983: The grouse of the world. — Croom Helm Ltd, London & Canberra.

Koivisto, I. 1965: Behaviour of the Black Grouse, Lyrurus tetrix (L.), during the spring display. — Finnish Game Res. 26:1–60.

Kruijt, J. P. & Hogan, J. A. 1967: Social behaviour on the lek in the Black grouse, Lyrurus tetrix tetrix (L.). — Ardea 55:203–240.

Kruijt, J. P., Vos, G. J. de & Bossema, I. 1972: The arena system of Black Grouse. — Proc. XVth Int. Orn. Congr, The Hague 1970:399–423.

Lewis, R. 1984: Density, movements, and breeding success of female Blue Grouse in an area of reduced male density. — Can. J. Zool. 62:1556–1560.

Noble, G. D. 1939: The role of dominance in the social life of birds. — Auk 56:263–273.

Nugent, D. P. & Boag, D. A. 1982: Communication among territorial female Spruce Grouse. — Can. J. Zool. 11:2624–2632.

Schoener, T. W. 1968: Sizes of feeding territories among birds. — Ecology 49:123–141.

Selous, E. 1909–10: Observations of the nuptial habits of the Blackcock in Scandinavia and England. — Zoologist 1909:400–413, 1910:23–29, 51–56, 176–182, 248–265.

Stirling, I. & Bendell, J. F. 1970: The reproductive behaviour of Blue Grouse. — Syesis 3:161–171.

Svensson, S. E. 1978: Census efficiency and number of visits to a study plot when estimating bird densities by the territory mapping method. - J. Appl. Ecol. 16:61–68.

Tinbergen, N. 1957: The functions of territory. — Bird Study 4:14–27.

Waser, P. M. & Wiley, R. H. 1980: Mechanisms and evolution of spacing in animals. — *In* Marler, D. & Vandenbergh, J.G. (eds): Handbook of behavioral neurobiology. Vol. 3:159–223. Plenum Publishing Corporation.

Wegge, P.: The spacing pattern and habitat use of radiomarked Capercaillie hens during the breeding season. — Proc. Third Int. Grouse Conf., International Council for Bird Preservation (in press).

Wittenberger, J. F. 1978: The evolution of mating systems in grouse. — Condor 80:126–137.

Received April 1985