

Social Behavior on the Lek in Black Grouse, *Lyrurus Tetrix Tetrix* (L.)

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SOCIAL BEHAVIOR ON THE LEK IN BLACK GROUSE, LYRURUS TETRIX TETRIX (L.)

by

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I. INTRODUCTION

The behavior of Black Grouse on their display grounds has often been described in both popular and scientific accounts. The main aspects of their breeding biology are well known (SELOUS 1909, 1910; LACK 1939, 1946; HÖHN 1953). Males assemble on a communal display ground,

¹⁾ Part of the investigation by Dr. J. A. HOGAN was carried out during the tenure of a National Science Foundation Postdoctoral Fellowship and during the tenure of a Public Health Service Fellowship (MPD-19, 133) from the National Institute of Mental Health. Present address of Dr. HOGAN: *Department of Psychology, University of Toronto, Canada.*

arena, or lek ¹⁾), especially during the early morning hours in spring. Each male defends its site from neighboring males by means of displays and, to a lesser extent, by actual fighting. Females visit the lek and are courted by the males. During these short visits the female chooses a male with which she mates. After mating the female departs and no further parental cooperation between the sexes takes place: nestbuilding, incubation, and care of the young are the exclusive task of the female.

The present paper is intended to amplify this picture, especially with regard to the following two questions.

a) What is the nature of the social organization of the males with respect to territories and their establishment, social hierarchy, and relative mating frequency?

b) What behavior is shown by the females, and what factors influence their choice of a mating partner?

In addition we shall take the opportunity to give more detailed descriptions of some behavior patterns than are hitherto available in the literature.

Our observations were carried out during spring 1961 and 1962 at a lek near *Fochtelo* (lek I) in the south-eastern part of the Province Friesland, Netherlands, the results of which have been reported briefly elsewhere (KRUIJT 1962; KRUIJT & HOGAN 1964). We continued our observations at lek I in 1963. Some additional observations were done in the spring of 1964 at this lek, as well as at a second lek (lek II) located at a distance of about 3 kilometers from the first. Both leks are situated in a series of meadows separated from each other by fences and sometimes by ditches. The centers of both leks are about 300 meters from the border of a large area of heather moorland in which the females nest. In late spring and summer the meadows of both leks are used for grazing cattle.

Although some of our observations were done in the late afternoon

¹⁾ The term lek has been derived from the Swedish word *leka* which means "to play" (ARMSTRONG 1964). Initially it was used in the English literature to indicate the display activities of the males; later, it was also used to indicate the communal display ground on which the activities occur. The latter usage will be followed in this paper.

FIGURE 1. Postures associated with threat and fighting at boundaries.

- A. Male to the left shows rookooing, male to the right in normal threat posture.
- B. Both males are in the posture which is accompanied by the fighting call.
- C. During jumping at each other males flap their wings and utter a hissing sound.
- D. Aggressive pecking is often directed at the opponent's head.
- E. At the end of a boundary fight males withdraw in display: the male to the left shows rookooing, the one to the right crows.

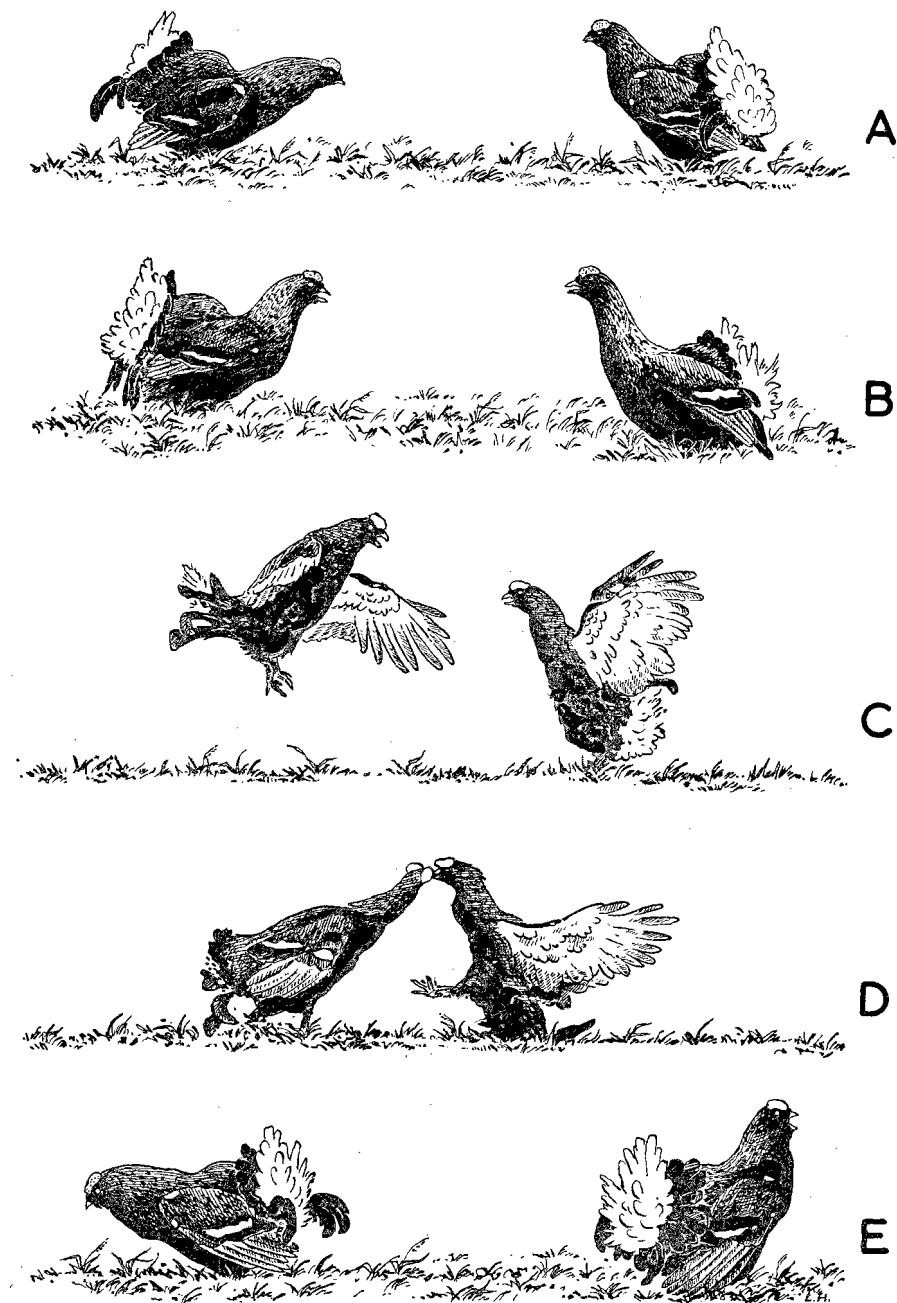


FIGURE 1. Text see opposite page.

when there is a temporary revival of activity on the lek, this paper is concerned only with morning observations. We usually started at about one hour before sunrise and continued for 2 or 3 hours after sunrise. Our data concern more than 80 mornings of observation divided over the years 1961-1964.

All observations were done from a hide, nearly always with at least two observers who divided the task of observing and recording. Numbered markers were placed at equal distances from each other on lek I in 1963 to facilitate a more precise recording of the positions and movements of the birds with respect to each other.

ACKNOWLEDGEMENTS

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II. BEHAVIOR OF MALES IN THE ABSENCE OF FEMALES

Males land on the lek about one hour before sunrise, either alone, or in a small group. Each male usually lands in the middle of his accustomed place immediately, but sometimes a male lands at a distance from his usual display site. In the latter case, the male invariably walks hurriedly to his own site. After reaching his own ground, a male usually starts to display immediately or within a few minutes. First the tail is erected and spread; this is usually followed by crowing and subsequently by rookooing. Each of the main patterns occurring during interactions of males will be described briefly.

We have followed the terminology of LACK and HÖHN to some extent but prefer to reserve the names describing sounds for the vocalizations alone, and to name the postures independently.

A. POSTURES

Horizontal display posture (Fig. 1A, left and 1E, left). In this attitude the tail is raised and spread, the wingbows are taken out of the supporting feathers, the primaries of both wings are extended downward slightly and the body and neck are held horizontally. The horizontal display posture is accompanied by rookooing (see below), during which the neck is inflated. This is the normal posture in which the males remain during most of their time on the lek.



FIGURE 2. Flutter-jumping.

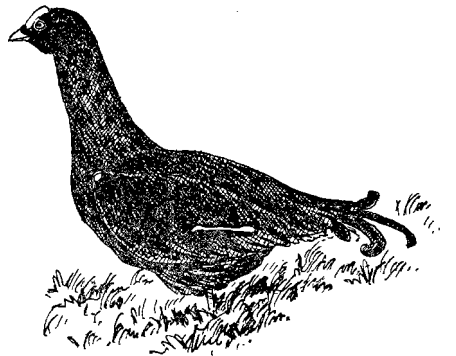


FIGURE 3. Alarm posture.

Erect posture (Fig. 1E, right). This is a variant of the horizontal display posture in which the neck is held vertically. In the erect posture the male may raise himself as much as possible, uttering a sound which has been called crowing (see below). In addition the wings are sometimes flapped.

Flutter-jumping (Fig. 2). The introductory part of flutter-jumping is identical to crowing in the erect posture, but instead of flapping the wings weakly, the male flies up to a height of 1 to 2 meters and over a distance of up to 10 or 15 meters. Simultaneously, the crowing sound is produced and repeated. During flutter-jumping the white underparts of the wings are very conspicuous. This pattern occurs frequently in response to the sight and/or sound of other birds flying over the lek or in its neighborhood. We have observed flutter-jumping in response to other bird species (e.g., flying ducks), but such "mistakes" occur only rarely when it is completely light. More usually it occurs as a response to flying Black Grouse, males as well as females, both when arriving and when departing from the lek. Flutter-jumping may also occur as an introduction to a fight with a neighbor which is about to trespass a territory boundary.

Alarm posture (Fig. 3). In this posture the tail is folded, the feathers are sleeked, and the body and neck are stretched upward. The alarm posture is shown primarily as a reaction to outside disturbances; it is shown also by intruder males (p. 217) during agonistic encounters with territorial males.

B. VOCALIZATIONS

Rookooing. This far reaching sound is the most conspicuous and most

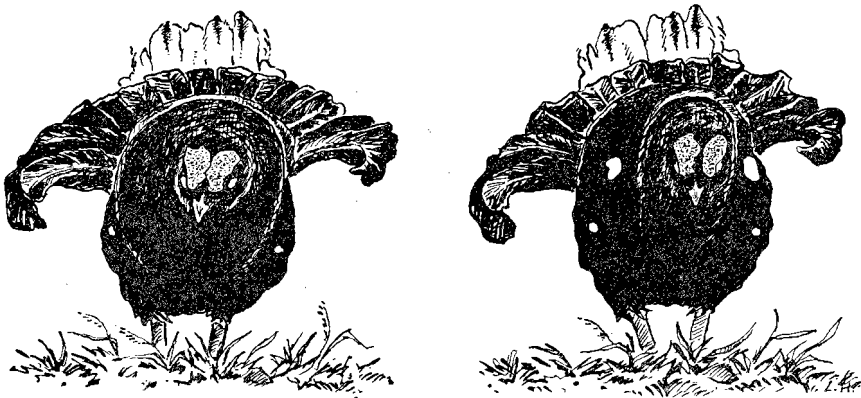


FIGURE 4. When seen from the front, the white wingbow-patches are alternately hidden and exposed as a result of inflation and deflation of the air-sacs during rookooing.

often described vocalization of the males. The sound is similar to the cooing of doves and pigeons, and strikes us as having 4 syllables which could be rendered as *rrooo-òò-rroo-rroo*. This strophe is repeated continuously for long periods. A spectrogram is shown in Plate VIII. The average duration of each strophe is about 3 to 4 seconds; the introductory part usually somewhat longer than that shown in this figure. Between every 2 strophes the bill is opened briefly and on cold mornings we observed that a small cloud of condensed breath is expelled at this moment. Apparently air is inhaled during the sound production and used air is exhaled in the brief intervals. Rookooing occurs in the horizontal display posture and during circling and squatting (display postures shown toward females and described on p. 219).

Rookooing (as well as other sounds) is probably an important auditory signal functioning during the interactions between males as well as between the sexes. In addition, visual signals from the conspicuous black and white markings of the males are produced during rookooing. As shown in Figure 4; the swollen neck vibrates rapidly; when seen from the front this has the effect that the white wing-bow patches appear to be flickering lights.

Crowing. This harsh hissing sounds to us as: *tsbooo-whch*; a spectrogram is shown in Plate VIII. Crowing occurs in the erect posture, during flutter-jumping, and during fighting with slight differences in the hissing sounds in each situation.

Fighting call. This, which sounds to us as: *koo-ke-rroo*, is frequently

uttered during threatening and fighting (Fig. 1B). It will be noticed that the spectrogram of the fighting call (Plate VIII) is very similar to that of rookooing.

C. AGONISTIC ENCOUNTERS

Males frequently threaten each other along the boundaries of the display sites. Threat consists of tentative approaches and withdrawals, performed in postures that vary between the horizontal display posture and a modification of this posture which contains elements seen in the erect posture (Fig. 1A, B). Crowing, rookooing, and the fighting call all occur frequently during threat. Such skirmishes usually do not lead to actual physical contact.

Sometimes, however, fights develop out of threatening. During fighting, males jump up at each other, often crowing simultaneously (Fig. 1C). Although the legs are used to kick the opponent, the bill is used more often; vicious pecking occurs often directed especially at the head of the opponent (Fig. 1D). In addition the fighting birds hit each other by beating their wings. Although blood may be drawn during fighting, this occurs only rarely.

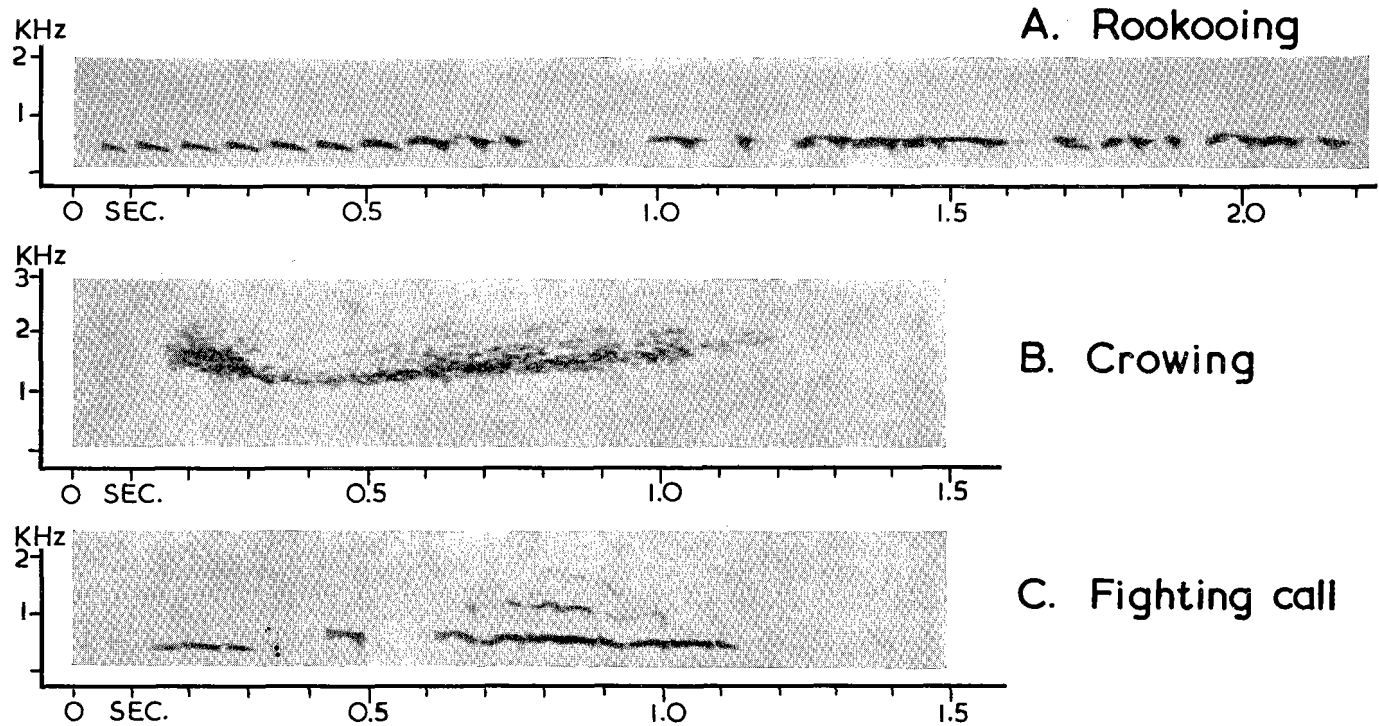
During threat and fighting, irrelevant movements occur. Head shaking is seen frequently; and, especially during prolonged threat, ground-scratching with one or both legs, and pecking at the ground or its intention movement were observed.

One bird, male H of lek B (see Fig. 5), showed an abnormal kind of behavior. During threats with his neighbors he frequently redirected his aggressive behavior toward his own tail. Often he ignored his opponent and turned round and round, all the time pecking viciously at the base of his own tail feathers. In Junglefowl such abnormal behavior may occur in individuals raised in groups in captivity, but it is a special feature of birds raised in isolation of conspecifics (KRUIJT 1964).

III. SOCIAL ORGANIZATION OF THE MALES

A. TERRITORIALITY

SELOUS has suggested that individual territories are defended by the males during the time that they fight and display, both when females are present and absent. This suggestion was confirmed by LACK and by HÖHN, although the former expressed some doubt as to the constancy of defended sites. LACK observed that disturbed cocks may shift their position over considerable distances while continuing to display and that



Spectrograms of the most common calls of male Black Grouse.

cocks seemed to be displaying in a rather different area during one visit than during another.

Our own observations have shown that many, but not all, males attending the lek defend territories. The behavior of non-territorial males will be described later (p. 216); we shall first discuss some aspects of the organization of territorial males.

On both leks that we observed, the territories could be clearly defined geographically and remained fairly constant throughout the season. Furthermore our three-year study of lek I showed great similarity in the location of territories from year to year. This is demonstrated in Figure 5, which shows the territorial organization of lek I from 1961 to 1963, and of lek II in 1964.

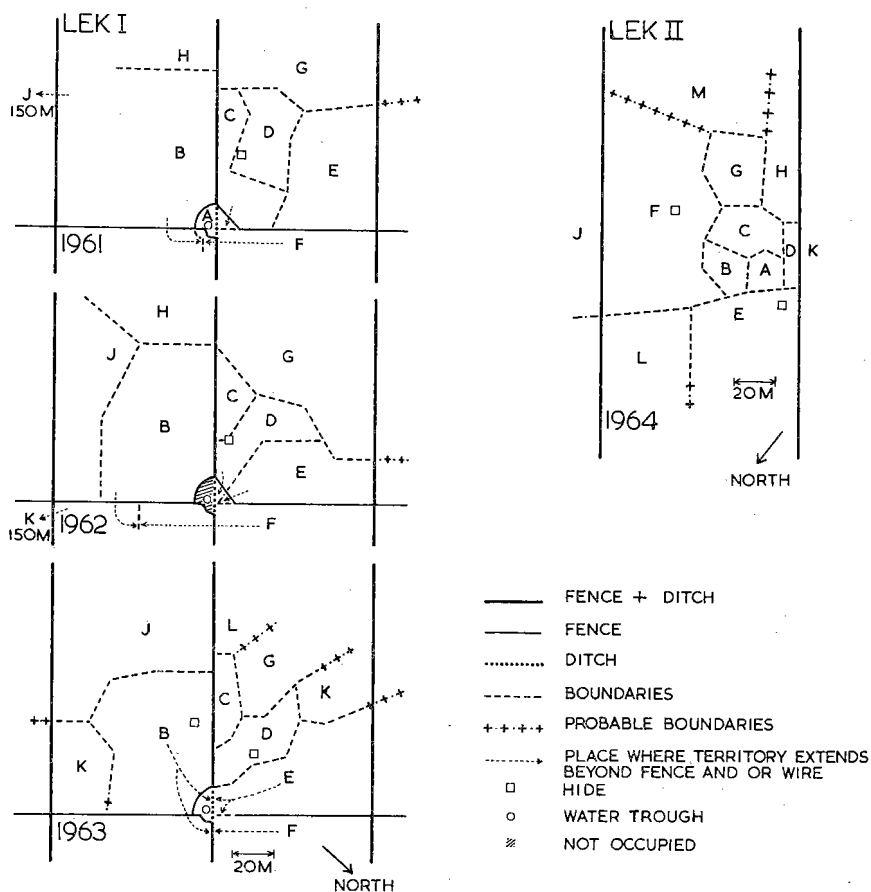


FIGURE 5. The distribution of territories on lek I in 1961, 1962 and 1963 and on lek II in 1964.

The boundaries of territories often coincide with landmarks present on the meadows, such as ditches and fences. Where this was the case, boundaries were omitted from the maps drawn in Figure 5. No conspicuous landmarks were present in the middle parts of the meadows, yet even here the boundaries remained remarkably constant; only slight changes of position were observed. The location of the boundaries could be most clearly determined at places where aggressive contacts between males occurred frequently. This was the case in the center of the lek where the territories were completely surrounded by ground claimed by other males. More difficulties arise toward the periphery because males meet each other only infrequently at the outside of the lek. As a criterion to estimate the size of such peripheral territories, we decided to consider as part of his territory ground on which a male displays often.

The average size of territories is estimated by both LACK and HÖHN to be on the order of 100 square meters; the largest territory observed by HÖHN measured 850 square meters. Our own measurements give considerably higher figures. The smallest territory we observed (male A on lek I) measured 100 square meters. All other territories ranged from 350 to over 4000 square meters on both leks. Toward the center of the lek territories tend to be smaller.

Correct identification of individual birds is of course a prerequisite for the construction of maps such as are shown in Figure 5. Ideally the birds should be marked, but we were unable to do this. Nevertheless individual males could sometimes be recognized by idiosyncrasies of behavior and/or by morphological features, such as bare patches on the plumage. Males which were recognizable in this way always showed great regularity in the location chosen on the lek and this convinced us that, with care, choice of location can be used to identify individuals if we could not recognize them in other ways.

This method gives, we believe, reliable results within one season, but the difficulties become greater if we want to follow the fate of individual males from season to season. For lack of a better method, we have, in drawing the maps of Figure 5, again used the location on the lek as a criterion. Thus, a male occupying a particular location on the lek was given the same name as the male occupying that location in the previous year. As judged from the constancy of the location in which rookooing and threatening occurred we feel that the males B, C, and D of lek I were probably the same individuals in all three years; with respect to males E, F, and G we are much less certain.

In two cases on lek I we have assumed identity from year to year even

though these individuals did not defend the same territories in successive years (males J and K). Our evidence in these cases is based on the fact that we saw these males change their location very gradually. For example, male J sometimes took his position of 1962 in 1961 and vice versa, and we saw this male shift from one position to the other within one session of observation. The evidence for male K will be described more fully later (p. 218). With respect to male J further evidence is available because in all three years this male produced a recognizable, abnormal kind of rookooing.

B. TERRITORIALITY AND SOCIAL HIERARCHY

Among social animals, at least three types of territorial communities have been distinguished (BAERENDS 1952) : (1) territorial society, in which every member defends a territory, the boundaries of which are mutually respected; thus, all members have equal rank; (2) dominated territorial society, like the previous type, but one individual is of higher rank and has access to the whole area; (3) hierarchical territorial society, like the previous type, but with a whole hierarchy of ranks.

It soon became clear during our observations that the lek of male Black Grouse conforms to the first type. Each of the territorial males has free access to his own territory only, and is, in general, victorious over every trespasser. Aggressive contacts along the boundaries are always undecided. Even if during a severe fight one of the opponents is driven back, the outcome will at most be that the boundary is slightly shifted at the cost of the worst fighter; in the end equality is reached again. Territorial males trespass only under exceptional circumstances (cf. p. 222) and are then chased out immediately. A trespassing territorial male usually flees immediately when being attacked, but starts to defend himself (and always successfully) as soon as he has reached his own ground. It can therefore be concluded that on the lek all territorial males are of equal rank; none has special privileges. An exception is formed by the non-territorial males (cf. p. 216). These males are usually chased out if they intrude into the ground of territorial males and sometimes they are chased far beyond the boundary that is normally maintained by the defending male. Thus, these non-territorial males can be considered to be lower in rank; they are at most tolerated if they stay away far enough and—as far as we know—such males are not able to maintain themselves successfully at any place.

We have often observed that a number of territorial males may fly

away as a group and land at a distance of several hundred meters where display may be continued. This occurs especially frequently after the birds have been disturbed on the lek. The display of birds outside the lek under these circumstances is of the same character as that occurring along the boundaries of territories: there is much mutual threatening and relatively little actual fighting. Non-territorial males may also join such a party. The aggressive contacts on such places are sometimes clearly decided in favor of one bird and the winner may chase the loser over considerable distances. In our observations it has never been possible to identify such individuals. In consequence we are neither able to say whether fights between territorial males are ever decided in favor of one of the two, nor, whether the relative positions of the birds under these circumstances bear any resemblance to the constellation of territories on the lek. Further observations will be necessary to find out whether a social hierarchy exists when flocks of aggressive birds meet on neutral ground outside the lek. But even if this is the case, a hierarchy does not exist on the lek itself; here all males must be considered to have equal rank.

In contrast to our own findings, BRÜLL (1961) has concluded that a hierarchial organization of Black Grouse males existed on the lek which he studied. He described a lek in which 2 groups of 4 males each displayed close together. According to BRÜLL, a clear linear hierarchy of dominance was distinguishable within each group of 4 males. Unfortunately no data are presented on which this conclusion is based; it appears from his report that outcome of fighting and mating frequency were not clearly distinguished as separate criteria to determine whether or not a rank order existed. It may therefore be doubted, pending further information, whether the social organization described by this author really differed from that observed by us.

Although we have concluded that territorial males are all of equal social rank, we have found it useful to divide them into two groups: central males and marginal males. No absolute distinction exists between these two groups; they should be considered as the extremes of one continuum. If we take the map of lek I in 1962 as an example (Fig. 5), males B, C, D and E are considered central males, whereas males F, G, H and J form the group of marginal males ¹⁾. We do not know which factors determine whether a male possesses a central or marginal position. Age and fighting abilities are probably both of importance; but this can

¹⁾ The status of male K will be discussed later (p. 218).

only be decided on the basis of long-term studies with marked individuals. The differences between central and marginal males can be characterized as follows.

(1) *Position and size of territories.* Central males have territories near the center of the lek; marginal males at the periphery. Central territories tend to be the smallest on the average. Furthermore, central territories are entirely, or for a great part, surrounded by territories of other males, while marginal males have territories with many 'open' boundaries. The larger size of marginal territories is of course partly due to this circumstance. If a new-coming male challenges property with 'open' boundaries (whether owned by central or marginal males) the defender usually yields part of his property, at least if the new-comer is persistent enough (cf. p. 219).

(2) *Attendance at the lek and site tenacity.* Central males often arrive at an earlier hour and depart later than marginal males; furthermore, central males usually remain continuously on the lek during the morning hours, whereas marginal males may be absent for short periods. Central males have the strongest site tenacity: they join a displaying party outside the lek (p. 214) less often than do marginal males.

(3) *Frequency of fighting.* Central males have many more aggressive contacts with neighbors than marginal males. An example is given in

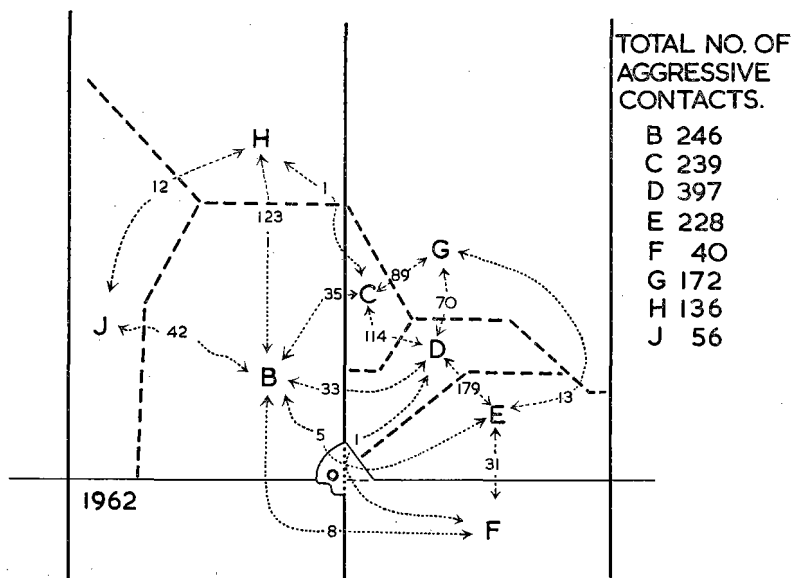


FIGURE 6. Number of observed aggressive contacts at boundaries on lek I in 1962.

Figure 6; it will be seen that many more fights and threats were scored for males B, C, D and E than for males F, G, H and J. The difference could be due to a higher level of aggression of the central males, or to the fact that these males are closer together and are therefore more strongly stimulated to fight (or to both). Fig. 6 also demonstrates that central males tend to fight more with each other than with marginal males. Thus, for example, C, D, and E have more aggressive contacts with each other than with marginal males. Exceptions to this rule occur, however, probably because the number of contacts between two males also depends on the length of the boundary that is shared by them and on the accessibility of the terrain at the boundary. For example, B had more contacts with the marginal males H and J than with the central males C and D, probably because the territory of B was separated by a ditch and fence from the territories of C and D.

It is interesting to note that a more complex social organization seems to exist in the North-American Sage Grouse (*Centrocercus urophasianus*). SCOTT (1942, 1950) has described a large lek attended by some 400 males. On this lek, four well-defined spots were distinguishable; on each, all cocks were dominated by one master-cock, assisted by a sub-cock and, still lower in rank, by 3 to 6 guard-cocks. These few cocks were surrounded by 60 or more other cocks which were considered to be the lowest in rank. But in this case again it is not entirely clear how dominance relations between the males were determined. At several places in SCOTT's papers one gets the impression that outcome of fighting was used as a criterion, but at another place (1942: 492) SCOTT mentions that on one morning "there were 10 matings by the master-cock, 8 by the sub-cock and 5 by the guard-cocks, the matter of dominance being gradually taken over in the order given". This gives the impression that males that mated most were regarded to be the dominant males. If so, then it is not correct of course, to conclude, as SCOTT does, that dominant males do most of the mating with the implication that dominance relations are determined by other criteria, viz. the outcome of fighting. The territorial organization in this species is also unclear. SCOTT believes that the master-cock maintains a territory, but it is neither clear from his description whether the sub-cock maintains a territory independent of the master-cock, nor whether the guard-cocks each possess their own area around the former two. Thus, although the social organization of this species seems to be more complex than in Black Grouse, a precise comparison is not yet possible. Further study of this and other North-American Grouse species would seem to be very rewarding for comparative purposes.

C. INTRUDERS AND THE ESTABLISHMENT OF NEW TERRITORIES

Males which had not established permanent territories are classified separately. These males are called the intruders, because of their tendency

to enter the territories of other males. Many, though not all, of the intruders were clearly juvenile birds: their combs were undersized and less intensively colored; they had short and only slightly bent tail-feathers and brown feathers on the wing.

BRÜLL (1961) has reported that none of these characteristics were present in an 8-month old male raised in captivity; he therefore concluded that external appearance may be deceiving with regard to estimates of age. We take this observation to mean that under some circumstances juvenile characteristics disappear at a relatively early age¹). Thus, absence of juvenile characters in spring may not be a reliable sign that the male in question is more than one year old. However—so far as we know—presence of such characters can be taken as a certain indication that the bird is a yearling.

In 1962 on lek I, the maximal number of intruders ever seen simultaneously was 4; 2 of these had juvenile characteristics. One of the intruders tried to establish a territory at the border of the lek and could therefore with reasonable certainty be identified by his location and behavior; this male was named K (cf. Fig. 5). In 1963 at least 5 intruders were present on lek I, 3 of which had juvenile properties; the other 2 males were K and L, both of which showed the beginnings of territorial behavior. The behavior of these 2 males will be described in more detail below.

Intruders usually come alone to the lek; more rarely a party of 2 or 3 arrived simultaneously. Only very rarely did they arrive together with females. Intruders come irregularly and the total duration of their presence on or near the lek is much less than that of marginal and central males. They were observed throughout our observation period in each year, both when females were present and absent. Intruders often wander irregularly around the border of the lek and frequently walk or fly into the more centrally located region. When females are present they often tend to take positions in their neighborhood, and show increased activity. They are often tolerated for a considerable length of time in the territories of other males, especially if they do not display but walk around quietly. Territory owners often ignore them under such conditions especially if they are themselves courting females. The intruders, however, will often start to display or to court a female (all the courtship patterns of territorial males were observed). If this is the case, the territory owner usually immediately initiates a fight or a chase. Only very rarely were intruders

¹) Three males which we raised ourselves were clearly of juvenile appearance at the first spring after hatching.

observed to show resistance when being attacked by central males (except K and L, see below). Thus, an attack by a central male on an intruder usually leads to a chase in which the former pursues the latter running or flying until well outside the territory (or even further). If intruders are attacked by marginal males (F, G, H and J on lek I) they do not always flee immediately but they may threaten and fight back. Intruders always lose these fights and are then chased out of the territory.

None of the males with juvenile properties were ever observed to defend a special place for a prolonged time. In consequence we were not able to follow the identity of these males from day to day. Two of the intruders, however, (both without juvenile properties) tried to establish territories; these 2 males are entered in the maps of Fig. 5. Their behavior will now be described in more detail.

Male K. In 1962 male K often displayed about 250 meters from of the center of lek I (Fig. 5). Females sometimes landed near him and K courted them. The females were never observed to crouch and stayed only for short times with him; usually they departed soon and visited the main lek. On 4 occasions that year K was observed to leave his place and to enter the territories of other birds. This male may have intruded more often, since he was sometimes not present in his accustomed place at times that intruders were present on the lek.

At the beginning of our observations in 1963 a male, presumably the same one, was present in the same place. K now often came closer to the border of the main lek region and started to display regularly in the southeast corner of B's field. From there he often intruded into the main lek area and visited the territories of all the other males. Here he often displayed or attempted to court females. Females sometimes visited him in the southeast corner; if these females headed for the main area he often followed them.

In the beginning of the season he was still often chased away from the southeast corner of B's field; in such cases K retired to the place where he displayed in 1962. From mid-April onward K started to defend the southeast corner against attacks of B and J and gradually he managed to hold his place. He still continued to intrude from this place into the other territories and did not always return to the southeast corner of B's field if chased away elsewhere. Instead he often retreated to a place north of the territories of E, D and G and from April 22 on he also started to defend this place. In the beginning of May he did not go to the southeast corner of B's field anymore, but spent most of his time north of D (Fig. 5) where he successfully defended himself against attacks by D, E and G. Occasionally he still intruded from there into the territories of other males.

Male L. This case provides a somewhat different picture of territory establishment. A strange male of adult appearance intruded into lek I on April 22, 1963. This male threatened and fought with B and J and although he lost, he remained on the lek, retreating to the west part of B's field. On the next day a male was fighting at the same place and he then crossed the ditch to a place

west of C. After much fighting with C, he maintained himself west of C and returned there on subsequent days. He managed to push the boundary of his territory eastward another 20 meters and returned there every day of our observations until the end of the season. Sometimes he left his territory and courted females in B's territory as well as east of it; he also intruded in other territories, returning to his own when chased away elsewhere.

The following tentative picture emerges from our data. It seems probable that as a yearling the male does not yet attempt to establish a territory. Instead he displays and courts all over and around the lek, in this way often entering the territories of other males. Fighting with other intruders and with marginal males does occur but is not yet restricted to a special location. This behavior is probably continued in the second year but in addition, the male now tries to hold ground at a special location usually at the periphery of the lek, or at some distance. From here the male attempts to extend his boundaries toward the center. During this time the male continues to behave as an intruder, which allows him to probe other potential territories. In consequence a male may then sometimes switch over to another place as was the case with male K in 1963. Our observations suggest that a male may be several years old before he succeeds in becoming a real territory owner. After the male has established a definite territory he probably does not intrude anymore, or only rarely, into other territories.

IV. BEHAVIOR OF MALES IN THE PRESENCE OF FEMALES

A. COURTSHIP AND MATING

Females usually approach the lek in flight and land either in the neighborhood or on the lek itself. To a flying female, males respond with flutter-jumping oriented toward her (p. 208). Subsequent behavior of the male depends in part on the position of the female. As long as the female is still outside his territory, the male usually continues rookooing in the horizontal display posture and walks in her direction, stopping at the boundary of his territory. In between the male may crow, or initiate a fight with a neighboring male. Frequently he squats at the boundary, facing the female.

Squatting (Fig. 7A). This pattern has been described as crouching by LACK and HÖHN. We reserve this term for the posture of the female prior to mating and prefer a different term for a similar pattern of the male because there are obvious differences between the two. Squatting is a modification of the horizontal display posture in which the legs are bent so that the bird is near the ground. The male continues rookooing

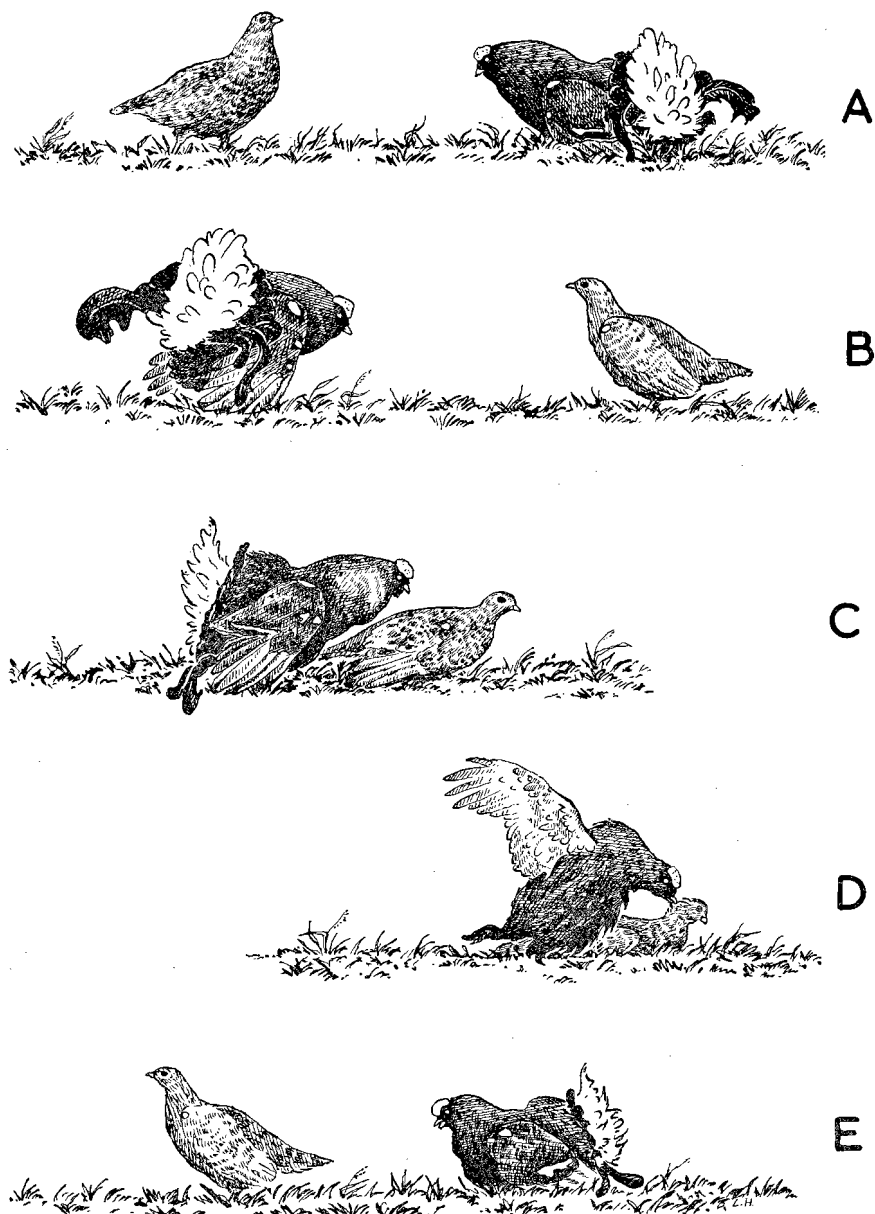


FIGURE 7. Courtship postures.

- A. Squatting. — B. Circling.
 C. The male mounts the crouching female in the circling posture.
 D. The wings are flapped during copulation.
 E. After copulation the male may continue to trample while the female withdraws quickly.

in this attitude, and may make a few small steps while continuing squatting. The primaries of both wings are extended downward and touch the ground.

Circling (Fig. 7B). During circling, the horizontal display posture of rookooing is adopted, but in addition the male lowers the primaries of both wings perpendicularly, so that these touch the ground. The primaries are also extended to some extent during interactions of males (Fig. 1), but during circling and squatting the extension is much more pronounced. In this attitude the male makes small rapid steps and attempts to walk around the female or females. HÖHN has reported that circling is performed silently; however we have found that males continue rookooing during circling right up to the moment of copulation.

Curiously enough, SELOUS, LACK, and HÖHN all mention that the tail is often tilted toward the female during circling. We have looked closely for this feature, but failed to observe it clearly, even after examination of our cine film. According to our observations the tail is kept roughly in a symmetrical position; a slight tilting occurs at most when the male circles at a sharp angle.

A male may start circling if a female approaches his territory but is still outside. Since the male usually stays inside his territory the circle cannot of course be completed in such cases. More usually the male continues to squat until the female enters his territory; at that moment circling often begins. The male may interrupt his circling to resume squatting even if the female is still in his territory. Fights with neighbors may also be interspersed; overt aggression toward the female, however, was never observed.

Copulation. In response to the courtship of the male, the female may crouch. If this occurs, the male completes his circle toward the rear of the female and mounts (Fig. 7C). Forced mating attempts were never observed. Only very rarely did mounting not occur as an immediate response to crouching of the female; on only one occasion did it appear that a male missed an opportunity to mate because of his hesitation after crouching of the female. Thus, the occurrence of copulation depends almost completely on the behavior of the female.

Model experiments with stuffed females (p. 235) afforded a good opportunity to observe the exact form of copulation. Typically a male circles closely around the model, and then turns toward the model at a right angle when passing a point straight behind it. He then mounts and sits in the copulatory attitude, usually holding the model's head-feathers (Fig. 7D). The male then tramples with his feet, often releases his hold

of the female's head-feathers, leans backward, flaps his wings vigorously, and attempts to make cloacal contact.

Mating with living females never lasted more than 7 seconds, the average being 2 seconds. After cloacal contact the female often struggles away from under the male and withdraws rapidly, ruffling herself; during this time the male often continues to sit in the copulatory attitude, raises his tail, and tramples with his feet (Fig. 7E). Subsequently the male often circles immediately around the same or another female. Squatting, or fighting with neighbors, also occur frequently after copulation. Successive copulations of the male, usually with different females (cf. p. 228), may occur with very short intervals; the shortest time observed was 15 seconds.

A central male does not follow the female as she leaves his territory; marginal males however sometimes do so, even if the female departs flying. Thus, central males show the strongest attachment to their territory, not only with regard to attendance to the lek and defense (p. 215), but also during courtship.

Intruders attempt to court females all over the lek; both squatting and circling were observed. Females that fly away from the lek are often followed by intruders. In cases in which the female landed within sight we have observed that marginal males or intruders may continue to court the female hundreds of meters away from the lek. We have never observed crouching of females on such occasions.

B. INTERFERENCE DURING MATING

LACK did not observe any real matings, but he reported that during mating with stuffed birds interference is not uncommon. We observed 9 cases of attempted mating with a mounted model (p. 235); during 5 of these a neighboring male crossed the boundary and attacked.

Interference occurs less often during real mating probably because it takes much less time than mounting on models (p. 235). Our data on interference during real mating are given in Table 1. Two classes of interference were distinguished. Cases in which a neighboring male crossed the boundary but did not contact the mating male until after the latter had dismounted were classed as impending interference; those cases in which the mating male was knocked off by the intruder were classed as actual interference. The last category was again subdivided according to whether or not cloacal contact had taken place.

For comparison, data on the Prairiechicken (*Tympanuchus cupido*), reported

TABLE 1

INTERFERENCE DURING MATING IN PRAIRIECHICKEN (*Tympanuchus cupido*) (AFTER HAMERSTROM 1960) AND BLACK GROUSE (*Lyrurus tetrix*).

Figures as % of total number of observed attempted copulations.

	Prairiechicken	Black Grouse
Number of attempted copulations	137	48
No interference	62.8	64.6
Impending interference	—	26.9
Actual interference	37.2	8.5
RESULT OF ACTUAL INTERFERENCE		
Mating disrupted	17.5	4.2
Mating not disrupted	16.8	4.2
Uncertain	2.9	—

by HAMERSTROM (1960) have been included in Table 1. It will be seen that:

(a) in both species actual or impending interference takes place in more than one third of the observed attempted copulations.

(b) mating is only rarely disrupted as a result of interference in Black Grouse but more frequently in the Prairiechicken.

V. BEHAVIOR OF FEMALES

A. VISITS TO THE LEK

During our four seasons of observations, females appeared regularly on the lek only between mid-April and the first days of May. Our earliest record of a female visit is on April 1 (none were seen during observations on 9 days in March); the latest record of a female visit is on May 11. Copulations occurred within a more restricted range: the earliest copulation we observed took place on April 14, the latest on May 5. More than 75% of all copulations occurred during the last 10 days of April. Figure 8 gives the distributions of number of females present on lek I and number of copulations observed throughout the season in 1961, 1962, and 1963. The fact that many of the females present on the lek do not copulate suggests that females visit the lek several times before copulating and may also visit the lek occasionally after copulating.

Females arrive on the lek early in the morning. The earliest arrival recorded was 43 minutes before sunrise; more than half of the females arrived earlier than 15 minutes after sunrise (Fig. 9). Time of arrival

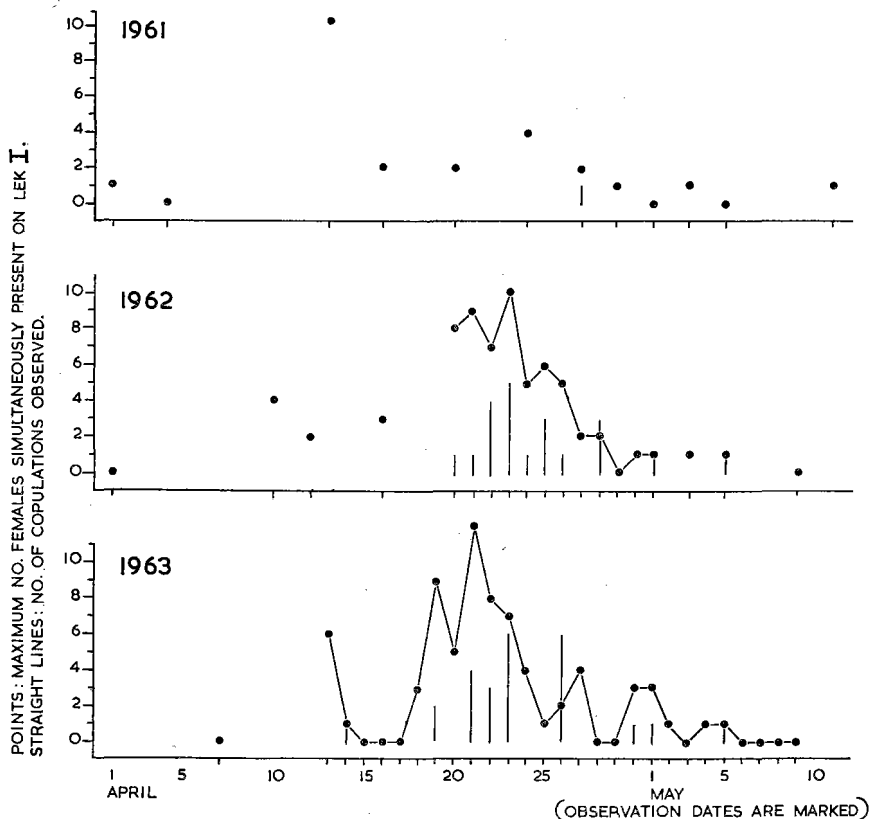


FIGURE 8. Observation dates, number of visiting females, and number of occurring copulations on lek I during three seasons.

showed considerable variability during the season. Our data for 1963 suggest that during the peak of the season (April 21-23) females arrive both earlier and later than during the rest of the season, but complete data on female arrival times from other seasons would be necessary before this conclusion can be considered reliable. Throughout the season, however, females that copulate arrive earlier than females that do not copulate; in 1963 the average times were about 3 minutes and 33 minutes after sunrise respectively (see Fig. 9). This difference is highly significant (Median Test, $P < 0.02$), and all the available data from other seasons strongly support this conclusion.

The few females that were seen early in April only visited the periphery of the lek and did not remain for a long time. By April 13, however, females landed on and visited all parts of the lek. Table 2 summarizes the

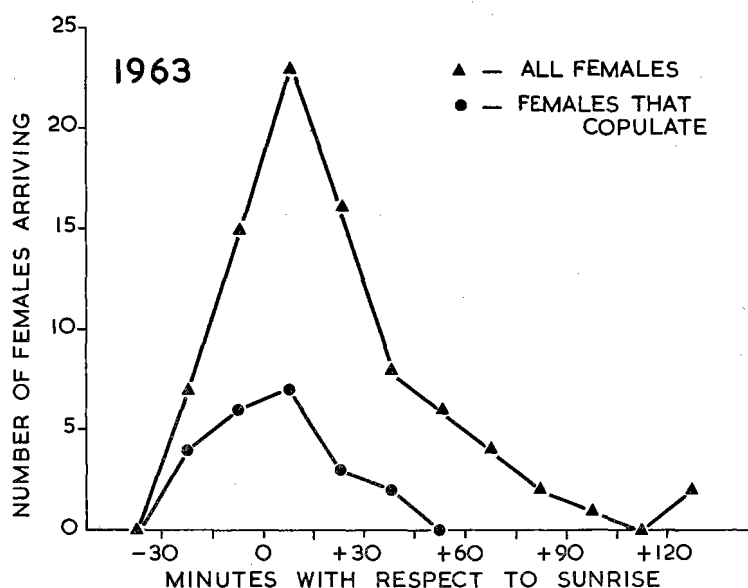


FIGURE 9. Frequency of female arrivals in relation with time of sunrise.

place of arrival of females during 1963. It should be noted that 53% of arriving females landed in one of the 4 central territories, even though these 4 territories comprise only 32% of the area of the lek (areas calculated from Fig. 5).

After arriving, a female generally begins to walk about the lek and visits several of the territories of the males, frequently returning to a particular territory several times. She may walk quickly or slowly and often stops to forage, preen, or crouch. It is very clear from the behavior of a female on the lek that although she is attracted, she also has a very

TABLE 2

AREA OF TERRITORIES AND PLACE OF ARRIVAL OF FEMALES ON LEK I IN 1963.

Territories	% area	Number of arrivals of females			
		April 3-20	April 21-23	April 24-May 5	Total
C and D	8	5	7	5	17 (20%)
B and E	24	7	12	9	28 (33%)
Others	68	14	13	12	39 (47%)

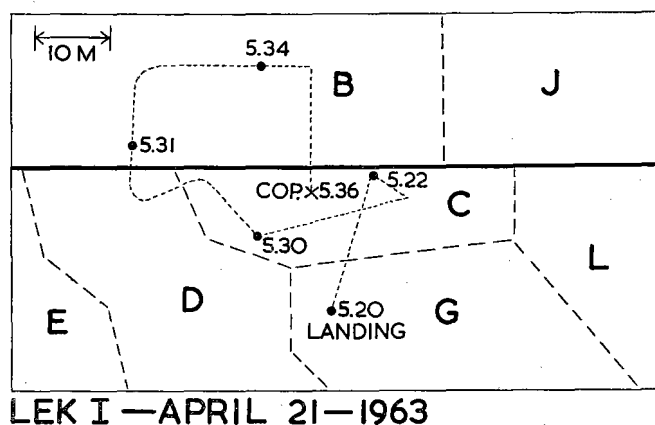


FIGURE 10. An example of female behavior during one visit from moment of arrival until copulation.

strong tendency to avoid a courting male, especially if the latter approaches too quickly. Crouching may occur in several territories and many times within one territory, but often the female withdraws at the very last moment, when the male is about to mount. This shows that the female does not make a single clear-cut choice. Instead, she makes several successive tentative choices; her final choice will be the place where she remains crouched just long enough to allow a male to mount and to mate. Females which have crouched during their visit may depart without having mated.

B. COPULATING FEMALES

During 1963 it was possible to follow the course of 16 of the 22 females that copulated during their visit, from the time of arrival until departure. These 16 females visited 1 to 13 (mean 3.5) territories¹⁾ and 1 to 6 (mean 2.5) different males before copulating. From arrival until departure these females visited 1 to 14 (mean 5.3) territories and 1 to 7 (mean 3.3) different males. Four of these females copulated with the male in whose territory they landed. Three of the 5 females that landed in the periphery walked immediately to one of the central territories; the other 2 arrived in the center within 5 minutes after landing. Figure 10 shows an example of a visit by a female. The distribution of visits to the individual territories and the total length of the visits are shown in

¹⁾ Each crossing of a boundary was scored as entering a territory even if the female had visited that territory before.

Figure 11. The great attraction of the center of the lek for females can be clearly seen from this figure. If the size of each territory (Fig. 5) is taken into account, these results are even more striking in that females make

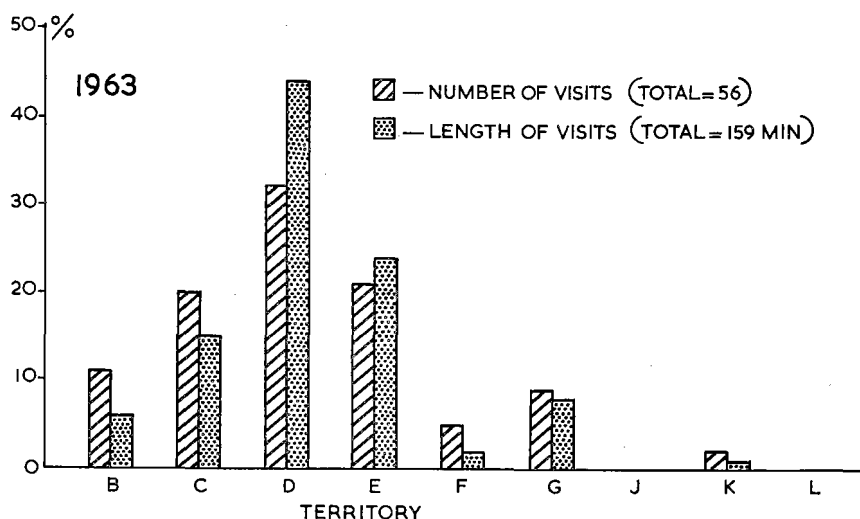


FIGURE 11. Number and length of female visits to the males of lek in 1963 (copulating females only).

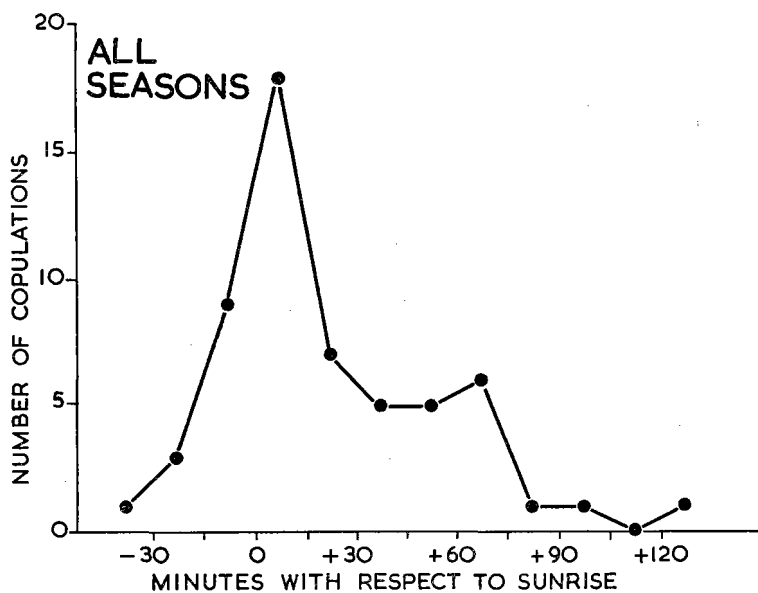


FIGURE 12. Frequency of mating in relation with time of sunrise.

the most visits and spend the most time in the smallest territories. Possible reasons for this preference will be discussed later (p. 230).

The distribution of copulation times over the 4 years is shown in Figure 12. It can be seen that frequency of copulation reaches a sharp peak just after sunrise, and that two-thirds of the copulations occur before one half hour after sunrise. More than 70% of the females that copulate do so within 15 minutes after landing on the lek. After copulating a female may fly away, but more usually she stays on the lek foraging or sometimes even visiting the territories of the males again. Females that have already copulated may crouch later for males, and on two occasions a female has been seen to copulate more than once in one morning. In 1962 a female copulated with 2 different males, and in 1963 a female copulated 4 times with the same male. In 1963 the average length of stay of females that copulated was about 50 minutes.

C. NON-COPULATING FEMALES

During 1963 it was also possible, in a total of 26 cases, to follow the course of an individual female that did not copulate from arrival on the lek until departure. These females visited 1 to 23 (mean 6.3) territories and 1 to 7 (mean 4.1) different males from arrival on the lek until departure. The pattern of their visits to the various territories was very similar

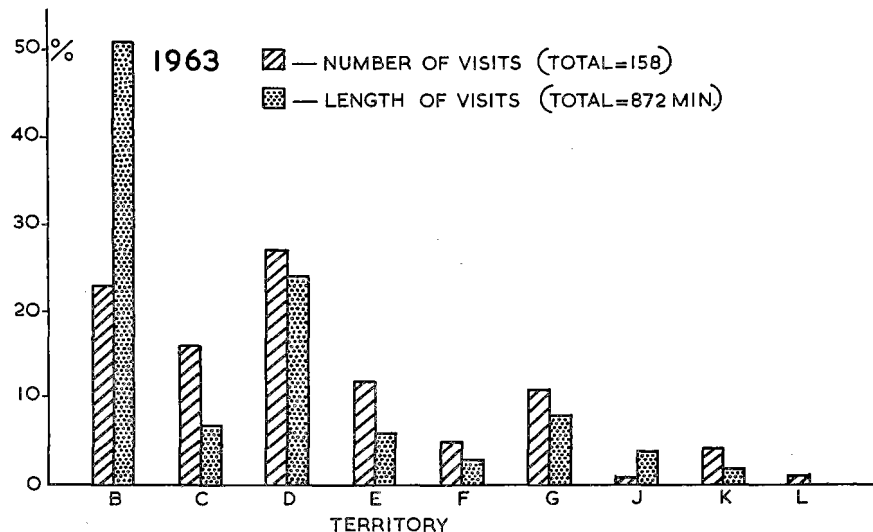


FIGURE 13. Number and length of female visits to the males of lek I in 1963 (non-copulating females only).

to the pattern shown by copulating females, but there was one notable exception. As can be seen in Figure 13, non-copulating females in 1963 spent almost 50% of their time in territory B. This very high proportion is due to the fact that most females appeared to find the northeast corner of territory B a good place for foraging. In 1963, non-copulating females remained on the lek an average of 52 minutes; this time is almost exactly equal to the time spent by copulating females.

The general picture that emerges from these data is that a female visits the lek on several mornings. Early in the season she may remain at the periphery but later she visits territories all over the lek and may start to crouch for males. On later occasions she visits fewer territories, usually in the center, during which time copulation takes place. After copulation the female begins foraging on the lek or its immediate neighbourhood. She may then resume her visits or fly away. If a female does not copulate during the first set of visits in the morning it is unlikely that revisits to the territories later the same morning will result in mating. Occasionally a female copulates more than once the same morning. It is quite possible that females visit the lek after the morning during which they copulate. From the total number of copulations observed during 1962 and 1963, and from the total number of females ever seen simultaneously either on the lek or outside the lek, one might estimate that each female copulates 2 times on the average in one season. However, the number of females may have been higher than we estimated; thus it is possible that most females copulate only once.

D. INTERACTIONS BETWEEN FEMALES

Although most of the behavior shown by females on the lek is either concerned with self-maintenance or directed with respect to males, females also show behavior directed toward or influenced by other females. On the one hand, females seem to be strongly attracted to other females. Not only do they frequently arrive or depart together, but females also are often found together in the same territory while visiting males, or while foraging. A female arriving alone on the lek regularly approaches and joins other females already present. (It is this tendency, in fact, that makes it so difficult for the observer to follow the behavior of an individual female). Furthermore, the presence of more than one female on a territory, or a female nearby on a neighboring territory, often seems to facilitate crouching and copulation, as suggested by the following example.

April 28, 1962 — 4.40 Female 1 lands between B and H; 4.41 to C, crouches;

4.45 to D; 4.46 to E, crouches; 4.50 to D; 4.52 to B; 4.54 flies to E; 4.55 to D, crouches; 4.56 to G, crouches; 4.59 to boundary between B and H; 5.00 to C; 5.01 to G; 5.02 to E; 5.03 to D, crouches; 5.11 to E; 5.12 to B; female 2 arrives on the lek, lands in C; female 1 flies immediately to C, crouches and mates; 15 seconds later female 2 mates with C. Both females fly away at 5.20.

Although females usually pay little attention to other females nearby, except that they stay close together, overt aggressive behavior between females occurs rather frequently. One female may suddenly raise and spread her tail, lower the primaries of her wings, and approach another female with a hissing sound. The posture is similar to that of males threatening at boundaries. The threatened female usually flees immediately. The threatening female may chase her adversary briefly, but such encounters rarely last more than a few seconds. On a few occasions mutual threatening was observed, and once a fight nearly developed; actual physical aggressive contact between two females, however, was never observed.

During 1962, 1963, and 1964, more than 60 cases of female threatening were recorded. Details of the other activities of the females during the same morning are available in 41 cases. These cases consisted of 25 threats by 11 females that copulated the same morning and 16 threats by 13 females that did not copulate the same morning. Using a t-test, this difference is significant at a level of 0.04. Thus, a high tendency to copulate is associated with a high frequency of threatening. With the present data, however, it is not possible to decide whether a tendency to threaten, regardless of frequency, is associated with a tendency to copulate. Such a comparison is very difficult because female threatening can only occur when two or more females are present in the same vicinity. Qualitatively such a conclusion seems likely because threatening occurs frequently just before or after crouching or copulation, while it occurs only very rarely when groups of 2 to 8 females are foraging on the lek.

VI. NON-RANDOM MATING: FACTORS UNDERLYING THE CHOICE OF THE FEMALE

The frequency of copulation of the individual males of lek I showed wide differences both in 1962 and in 1963: frequency distributions are shown in Figure 14. It can be seen that B, C, D and E, the 4 most central cocks, performed more than 85% of the copulations in both seasons, while the 5 or 6 other males performed less than 15% of the copulations. The latter were performed by males F and G, both of which were marginal males. Intruders (males K and L, and the unnamed ones) were never observed to copulate. Similar data were obtained in 1964 on lek II.

Possible explanations of these differences will be considered in this section.

A simple explanation of differences in frequency of copulation would be that the probability that a male will mate with a female is proportional to the amount of time she spends in his territory. The data for the number of visits and the amount of time spent in each territory by females that copulate are very similar to the data for the frequency of copulation of the various males (see Figs. 11 and 14). This suggests that the probability

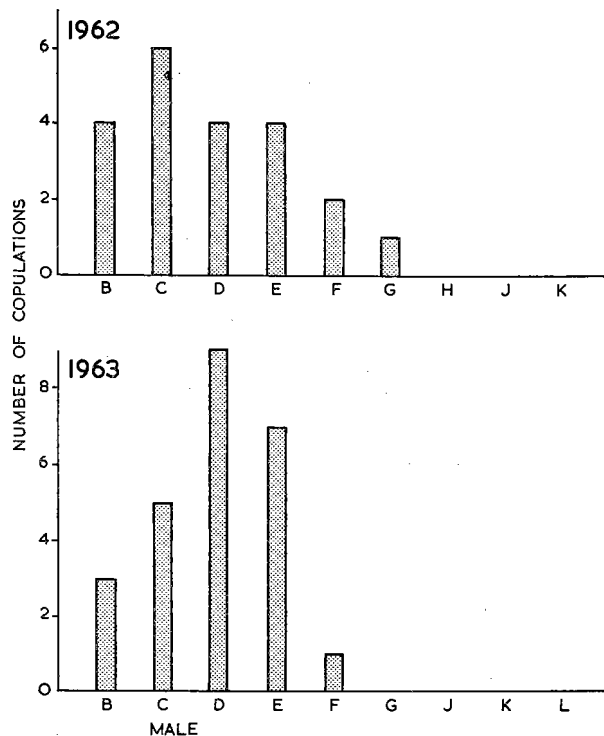


FIGURE 14. The distribution of mating over the males of lek A in 1962 and 1963.

that a male will copulate with a receptive female is, indeed, proportional to the amount of time the female spends in his territory. The problem of the choice of the female is then reduced to discovering which factors influence entering and remaining in a territory; and, in particular, which factors determine the great attractiveness of central territories. Since central territories are neither more numerous nor larger than marginal territories (p. 215), their attractiveness cannot be due to a random effect; several other possible factors will be considered here.

(a) *Physical features of the terrain.* Such a factor seems very unlikely to have been of influence on either of the two leks we observed since both leks were situated on level meadows. It is true that the center of lek I lay along a small ditch in which females appeared to spend considerable time while visiting the lek, but ditches were also located at the periphery of the lek; further, ditches were located at the periphery of lek II even though the center was completely void of any noticeable characteristics.

(b) *Differences in behavior of central and peripheral males* before the female has landed. At the time that a flying female approaches the lek, males show very intensive flutter-jumping (Fig. 2). Although we have no quantitative data, our impression is that all males usually participate strongly in this. Thus there is no reason to believe that differences in behavior play an important role in determining where the female will land.

(c) *Density of conspecifics.* A density factor might be very important in determining where a female mates if, for example, the presence of conspecifics reduces her tendency to fly away from the lek. A female arriving by air could easily discriminate density even from a considerable distance because of the flutter-jumping of the males. Once having landed she could also easily see that males are more concentrated in some places than in others. The data given above on the mutual attraction of females supports the idea that density is an important factor; data given below in the next section can also be interpreted as support for a density factor.

(d) *Differences in behavior of central and peripheral males: general activity.* During the course of our observations, females were seen to approach fighting males on many occasions. On one day at the end of the season in 1963 there was only one female present on the lek; the course of her movement over the lek on that morning during one and a half hours gave the impression of being almost completely determined by the location of fighting males. On days with more activity it would be much more difficult to see such a correlation, though our impression is that females approach fighting males more than they withdraw from them. The attractive feature of fighting males could be the fighting as such or, more generally, the heightened activity of the males. Another possibility is that fighting males are attractive because at least two males are close together during fighting; thus, density would be of importance. Very likely, both factors play a role.

(e) *Differences in behavior of central and peripheral males: tactics.* Females

seem particularly attracted to squatting males, and a male that squats near the edge of his territory facing a female in a neighboring territory has a greater chance that the female will approach him than if the male is rookooing or crowing at some distance. Squatting at a distance from a female that is walking out of a male's territory frequently has the effect that the female stops and thus remains in this territory; circling between a female about to leave a territory and the boundary with a neighboring territory often has the same effect. Further, close circling tends to stimulate a receptive female to crouch more than circling at a greater distance. On the other hand, females that are not yet ready to crouch, are more likely to remain if the male squats or makes wide rather than close circles. Thus, efficient timing of squatting and circling at various distances with respect to the behavior of the female could easily have a large influence on the amount of time she spends in his territory. Our data indicate that some males are, in fact, more or less efficient than other males. The protocols for males C and D of lek I typically show almost perfect tactics: as soon as a female enters their territory, they circle very closely immediately; if the female shows signs of crouching they continue circling; if, however, the female starts to walk away, they immediately withdraw to a distance of 3 to 5 meters and squat; when the female stops walking or approaching they immediately begin circling again; and so on. Sometimes, of course, the male will continue close circling when the female begins walking; but the usual effect of such behavior is that the female leaves the territory immediately. Male B tends to show considerably less perfect tactics: he frequently does not approach a female that has just entered his territory; he often circles and squats at distances of more than 15 meters from the female; and he very frequently continues circling when a female begins to walk. Males F and J rarely pay much attention to females in their territory, and if these males do begin circling, they usually cease within several seconds even if the female shows no signs of leaving. A quantitative picture of tactics would require many samples of an individual male's behavior both in the presence and absence of females. Since we tended to concentrate our attention on the individual females our data on this point unfortunately do not lend themselves to a rigorous analysis.

Assuming that tactics is actually an important factor determining where a female will mate, there are at least two possible mechanisms which could account for a male having superior tactics. First, more successful males may have a better "balance" of drives. For example, if a central position on the lek is due to high aggressiveness of the individual,

this latter factor might also influence the male's behavior toward the female in such a way as to make it more effective. A second possibility is that a male could learn over a period of years what influence his actions have on the behavior of the female. For example, he could learn that squatting at a distance frequently causes the female to stop walking. Observations of individual males over several seasons and learning experiments with moving models on the lek could give data which would throw more light on these and other possible mechanisms underlying tactics.

The problem of female choice is probably further complicated because she visits the lek more than one time: it is possible that events during earlier visits will influence her behavior during later visits. Thus, for example, if a female lands in the center of the lek then this may be due to characteristics of the situation at that moment, such as, for example, the higher density of the males in the center. On the other hand, it is also possible that poor tactics of marginal males during previous visits of the female caused her to land and to remain in the center during a subsequent visit. Whether such long term processes play a role can only be examined by working with marked females over longer periods of time. It may be noted that copulating females tend to visit fewer territories and fewer males than non-copulating females (p. 226); this suggests that long term changes in the behavior of the females indeed do take place.

Concluding this section, we may note that SCOTT (1942) has shown that in Sage Grouse (*Centrocercus urophasianus*), 87% of the matings are performed by less than 3% of the cocks present on the lek. This contrasts rather strongly with Black Grouse where we have found that about the same proportion is performed by about one third of the cocks that are maximally present on the lek. The two species have in common that mating is non-random and this effect is brought about by choice from the side of the female. SCOTT seems to believe that females select the most dominant males. As discussed earlier, it is not entirely clear whether it is correct to consider certain males more dominant than others in this case (p. 216). But even if this were so, it would still remain obscure how females identify dominant males.

In the case of Black Grouse, we find that females prefer males that have territories at the center of the lek. Neither physical characteristics of the terrain, nor behavioral differences of central and marginal males before the female has landed, are likely to be of much importance in determining the great attraction of the center. Of more importance are possibly the greater density of males in the center and, after landing of the female, the tendency of central males to show more mutual interac-

tions and better tactics; further study is however necessary to elucidate this problem.

VII. MODEL EXPERIMENTS

LACK has presented stuffed male and female models on the lek and found that males attempted to copulate with the latter whereas the former were either ignored or attacked. We performed a number of similar experiments between April 19 and May 8, 1963 on lek I. A male and a female model both mounted in the crouched posture were each presented 15 times ¹⁾.

Male model. The male model was ignored or elicited slight alarm in 12 of 15 cases. In the remaining cases the model was attacked two times and in one case a male attempted to copulate with the model. The latter case was concerned with male C which had ignored the model for 20 minutes and then attempted to mate after a female which he had courted vigorously had left his territory. Probably, the tendency to mate was released by the living female in this case and was then redirected to the male model when the female left C's territory. Aggressive behavior toward the model is similar to that occurring along the boundaries of a territory. The attacking bird starts to threaten and next, charges occur, which are stopped short at the last moment. Subsequently the attack may be continued with vicious pecking, mainly directed to the head of the model. The fighting call is usually uttered all the time. Wing-beating is less common than in fights between living males.

Female model. The female model was ignored 7 times; in the remaining 8 cases males attempted to copulate. We can confirm LACK's observation that under this condition males seem unable to stop their attempts to mate. One male showed mounting attempts for 2 hours and in none of the other cases were mating attempts terminated in less than half an hour.

Whereas mating with living females never lasted more than 7 seconds, and usually less, attempts to make cloacal contact with the uncooperative model sometimes lasted up to half a minute. After one such an attempt the male often pecked at the model's head, dismounted, and circled the model. Renewed mounting often followed immediately after completion of one circle. After a number of such attempts the male usually withdrew to a distance of one to several meters and squatted for a while, facing the model, after which he would again circle and attempt to copulate. Complete copulation attempts (i.e. including the final stage of trampling, wing-flapping and attempts to make cloacal contact) became rarer later in the series of mounting. Instead the male would then often mount and continue to rookoo without assuming the copulatory attitude; he would then dismount and circle.

¹⁾ A piece of wire was connected to each leg of the stuffed bird; these could be stuck into the ground, giving the model the necessary stability. Each model was generally presented under a cloth which was connected to a string leading to the hide. In this way the model could be exposed at the desired time by pulling off the cloth.

Male D mounted over 50 times during 45 minutes before he ceased to respond to the model—probably distracted by the arrival of a living female. Later he resumed mating attempts for another 15 minutes. In the first series of his mountings he showed complete copulation attempts 5 times, while trampling only was performed 6 times; the remaining cases were limited to mounting with or without brief adoption of the copulatory attitude. In another case D was observed to show 26 copulation attempts in one hour; in addition he mounted the model 68 times without attempts to make cloacal contact. The duration of complete copulation attempts decreased from 16 seconds in the beginning of the series to 2 seconds in the last part.

Although both central and marginal males reacted to the models, not enough experiments were done to decide whether the two groups show differences; qualitatively the reactions were the same.

We plan to do further experiments with models in which apart from the sex of the model, position on the lek, posture of the model, and time of presentation during the season will also be varied. A full discussion of the present results will therefore be postponed, but two conclusions seem clear. First, although the crouching posture of the female is important in releasing copulatory behavior of the male, morphological properties play an important role in addition. Second, the prolonged mating attempts with female models suggest that males have a very strong copulatory tendency; a decline of this tendency is not likely to occur rapidly.

VIII. ANNUAL PERIODICITY

It is generally believed that there are 2 main periods of activity on the lek, from February to May, with a peak in April and a secondary one in October. We have no data concerning the autumn period, but we visited lek I at the time of sunrise on June 29, 1962; January 16, 1963 (when deep snow was covering the lek); and August 22, 1964. We observed 14, 10 and 9 cocks respectively on these dates. Lek II was visited on August 22, 1964; 14 males were present. On the day at the end of June all males kept to their usual territories and several boundary threats were observed; rookooing occurred until about one half hour after sunrise. Normal territoriality was much less clearly present in January and August. Some of the males were present at their usual places, but others kept more or less together as a group in a meadow neighboring the lek. Mutual threatening was fairly frequent, a few fights were seen, and at least one male was observed to rookoo faintly for a short period on both dates.

It seems probable from these observations that the territorial males

visit the lek throughout most of the year and that non-territorial males may also be present. Outside the spring and autumn period the visits are probably always short, possibly limited to the time just after sunrise, and display is of much lower intensity.

The presence of males on the lek outside the spring period (e.g. in the autumn) has sometimes been considered functionless (LACK, 1939). However, in our opinion this fact can also be considered as indicating the existence of strong selection pressure for attachment to the lek and for territoriality. Maintenance of territorial ownership is probably strongly facilitated by such short visits to the lek continuing the whole year round.

SUMMARY

This paper presents data gathered in four spring seasons of observations at two Black Grouse *leks* in the northern Netherlands. Behavior of males among each other, of females, and courtship and mating are described.

Roughly two-thirds of the approximately 12 males attending each lek were *territorial*; the remaining males were *non-territorial*.

Territorial males defend geographically fixed areas, varying in size from 100 to over 4000 square meters. Territories remain highly constant throughout the spring and fairly constant from season to season. All territorial males have access to their own territory only and trespass only under special circumstances; on the lek they are therefore by definition of equal rank. Territorial males can be classified roughly as *central* and *marginal males*. The former tend to have smaller territories at the center, are more continuously present on the lek, display less frequently outside the lek, and show a higher frequency of aggressive behavior than marginal males.

Non-territorial males are called the *intruders* because they frequently enter the ground of territorial males where they are usually chased off; they are therefore considered to be lower in rank than territorial males. Most, though not all, intruders are juvenile males. Intruders attend the lek irregularly; when present, they may show all the same fighting, threat, and courtship patterns as territorial males. By persistence an intruder may establish a new territory at the edge of the lek; two such cases are described.

Females start to visit the lek regularly in April; most of the mating takes place in the second half of April, usually around the time of sunrise. When a female visits a territory, the owner courts her by squatting at a distance and by circling her, which may lead to copulation. Neighboring males attempted to interfere in more than one third of the observed copulations, but this leads only rarely to actual disruption of the mating.

During their visits to the lek, females walk from territory to territory and have a strong tendency to stay together in groups. Tentative crouching in response to courtship of the males may occur in several territories and many

times within one territory. Females often terminate crouching and withdraw at the moment that a male attempts to mount. By crouching long enough a female allows a male to mount and mate; in this way she exerts her choice. Females sometimes mate more than once during a visit; in one case a female was observed to mate with 2 different males.

Analysis of landing and visiting distributions show that females prefer central territories at the peak of the season. More than 85% of the copulations was performed by central males; the remaining by marginal males. Factors underlying the preference of females for central males are discussed. The choice of the female is possibly influenced by the greater density of males in the center and by the tendency of central males to show more mutual interactions and better tactics during their courtship.

The *annual periodicity* of lek display is discussed briefly; it appears that Black Grouse males visit the lek during most of the year.

Some results of experiments with *stuffed models* are described.

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SAMENVATTING

In dit artikel worden waarnemingen behandeld die werden verzameld gedurende vier voorjaarsseizoenen op twee baltsplaatsen of *leks* van *Korboenders*. Beide leks bevinden zich bij het Fochteloërveen in Friesland.

Ongeveer twee-derde van de 12 hanen die zich op iedere lek bevonden waren territoriaal, d.w.z. deze hanen verdedigden een bepaald stukje grond tegen naburige hanen. De andere hanen bezaten zulk een grondgebied niet.

Het kleinste *territorium* mat ongeveer 100 m², het grootste meer dan 4000 m². De grenzen van deze territoria veranderden maar weinig gedurende ieder voorjaar en bleven zelfs van jaar tot jaar tamelijk constant. Alle territoriale hanen hadden ongehinderd toegang tot hun eigen territorium; zij overschreden hun grenzen alleen onder bijzondere omstandigheden en werden daar dan door naburige hanen verjaagd. Aangezien geen enkele van deze hanen speciale voorrechten geniet voor wat betreft de toegankelijkheid tot andere territoria kan geconcludeerd worden, dat zij blijkbaar alle op de lek dezelfde sociale status of rang bezitten, hoewel de mogelijkheid bestaat dat buiten de lek verschillen in status bestaan. De territoriale hanen kunnen worden onderverdeeld in *centrale hanen* en *randhanen*. Hoewel het onderscheid tussen beide klassen niet altijd scherp te trekken is, kunnen zij worden onderscheiden doordat de centrale hanen in het algemeen kleinere territoria in het centrum van de lek hebben, doordat zij vaker en langer op de lek aanwezig zijn, doordat zij minder vaak buiten de lek baltsen, en doordat zij vaker dan de randhanen agressief gedrag vertonen.

Hanen zonder territorium worden *indringers* genoemd omdat zij vaak het grondgebied van territoriale hanen binnendringen waar zij meestal worden weggejaagd; om deze reden wordt geconcludeerd, dat deze hanen (die vaak, hoewel niet altijd, éénjarig zijn) een lagere sociale status hebben dan de territoriale hanen. Indringers zijn vaak afwezig; zij bezoeken de lek op ongeregelde tijdstippen. Wanneer zij aanwezig zijn kunnen zij dezelfde vecht-, dreig-, en baltsgedragingen vertonen als territoriale hanen. In de loop der tijd kan een indringer van status veranderen door zich een territorium te veroveren, meestal aan de rand van de lek. Twee van dergelijke gevallen worden beschreven.

De *hennen* beginnen de lek regelmatig te bezoeken in april; de meeste copulaties vinden plaats in de tweede helft van april, gewoonlijk omstreeks zonsopgang. Bij het bezoek van een hen aan een territorium vertoont de bezittende haan speciale balts-handelingen: de *omlaag houding* en het *cirkelen*, welke laatste handeling kan leiden tot de copulatie. Beide handelingen worden begeleid door het koeren dat echter ook bij afwezigheid van hennen optreedt. Naburige hanen probeerden te interfereren in meer dan een derde van de waargenomen copulaties, maar dit leidde slechts zelden tot een werkelijke interruptie.

Gedurende hun aanwezigheid op de lek bezoeken de hennen meestal verscheidene territoria en zij hebben daarbij een sterke neiging elkaar op te zoeken en in groepjes rond te lopen. De hennen beantwoorden de balts van de hanen o.a. door te hurken; zij kunnen dat bij verschillende hanen doen en vele malen bij eenzelfde haan. Wanneer een cirkelende haan een hurkende hen benadert en tracht op te stappen, beëindigt de hen vaak de hurkhouding en ontloopt de haan. Door te blijven hurken stelt zij de haan in staat om op te stappen en te copuleren; op deze wijze bepaalt de hen tenslotte haar keuze voor een copulatie-partner. Hennen copuleren meestal éénmaal per bezoek, in enkele gevallen meer dan eens. In één geval werd waargenomen dat een hen

gedurende haar bezoek met twee verschillende hanen copuleerde. Waarschijnlijk brengt de hen slechts één- of tweemaal een bezoek aan de lek waarbij een copulatie optreedt.

In het hoogseizoen hadden de hennen een duidelijke voorkeur voor de territoria die in het centrum van de lek waren gelegen. Meer dan 85% van de copulaties werd volvoerd door de centrale hanen; de rest door randhanen. Er werden geen copulaties van indringers gezien. De factoren die ten grondslag zouden kunnen liggen aan de voorkeur van hennen voor centrale hanen worden besproken. Mogelijk wordt de keuze van de hen beïnvloed door de grotere dichtheid van hanen in het centrum, door de neiging van centrale hanen om onderling meer agressieve contacten te hebben en doordat centrale hanen gedurende de balts een betere tactiek tegenover de hen vertonen. Verder onderzoek is hierover nodig.

De *jaarlijkse periodiciteit* van het baltsvertoon op de lek wordt kort besproken. Waarschijnlijk bezoeken territoriale korhanen de lek iedere dag gedurende het grootste deel van het jaar. Enkele resultaten van proeven met opgezette korhoenders worden beschreven.