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Territoriality and Non-Random Mating in Sage Grouse, *Centrocercus urophasianus*

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I. INTRODUCTION

The extreme polygyny practised by sage grouse *Centrocercus urophasianus* (Tetraonidae) was first described by Scott (1942) and subsequently confirmed by Patterson (1952) and Lumsden (1968). Of 355 males that Scott observed on one communal display ground, or lek, only a few 'master cocks' performed 74 per cent of all recorded copulations. The females formed dense aggregations each morning at a few sites on the lek. Because almost all matings occurred there, Scott termed these sites mating centres. The few males that maintained positions in these packs of females performed almost all the matings.

Despite the early recognition of the non-random distribution of matings among male sage grouse, the behavioural regulation of this mating system has remained unclear. Scott, Patterson and Lumsden recognized that individual males tended to return each morning to the same positions on a lek, yet none of these observers interpreted the males' interactions in terms of territoriality. Scott (1942), without describing the males' interactions quantitatively, implied that mating was regulated by a dominance hierarchy among the males. He referred to those males successful in mating as 'master cocks', or 'dominant' males. Lumsden (1968) managed to mark individually several males that he captured by cannon-netting on their lek immediately before he began his observations. He reported that these males subsequently occupied overlapping areas on the lek and felt, therefore, that these areas could not be considered territories. He also eventually concluded that the behaviour of males on a lek best fits the notion of a dominance hierarchy.

Moreover, the females that Lumsden observed during the month of his study showed little of the faithfulness to a particular mating centre that had been described earlier by Simon (1940), Scott (1942) and Patterson (1952). Instead, the females observed by Lumsden gathered at many different places on the lek and at different places on different mornings. His observations are not altogether conclusive, since cannon-netting the birds on a lek might change their fidelity to the sites where they had been trapped. Although Lumsden observed three males that occupied roughly the same area in which they had been cannon-netted a year before his study, Dalke et al. (1963) suggest that some but not all males might leave their positions after being cannon-netted. Females might react even more strongly than males.

In several other lek-forming species of grouse, the males' interactions show clear resemblances to classical territoriality: black grouse *Lyrurus tetrix* (especially Koivisto 1965; Kruijt & Hogan 1967; Hjorth 1970); sharp-tailed grouse *Pedioecetes phasianellus* (Lumsden 1965; Evans 1969; Trobec & Oring 1970); and prairie chickens *Tympanuchus cupido* (Hamerstrom & Hamerstrom 1960). Male black grouse occupy small, but largely exclusive, territories on a lek, and neighbours encounter each other along mutual boundaries. Yet in all these species, as in sage grouse, successful matings are distributed unequally among the males.

Thus it remains unclear whether ordinary conceptions of dominance hierarchies or territoriality apply to the social interactions of male grouse on their leks. The crux of the problem is how can we reconcile the localization of the males on a lek, which suggests territoriality, with the non-random distribution of matings among them, which suggests a dominance hierarchy? Kruijt & Hogan (1967) have begun quantitative observations of social interactions on black grouse leks, but nothing similar has been attempted for sage grouse. As sage grouse show an extreme form of a lek mating system, a better understanding of their behavioural interactions might suggest principles that would help understand other species as well.

This paper is particularly concerned with the dominance hierarchy and the territory as paradigms for social interaction on sage grouse leks. The immediately following section will introduce the concept of polarity in social interactions as a basic distinction between classical conceptions of dominance hierarchies and territoriality. The body of this paper will then explore the behaviour of male sage grouse on their leks, in an attempt to quantify the interactions that might regulate the species' mating system. The nature of the polarities in the males' interactions will reveal the special fusion of territorial and hierarchical organization on a sage grouse lek.

II. DOMINANCE HIERARCHIES AND TERRITORIALITY: INTRODUCTORY REMARKS

A. Polarity in Social Interactions

Differences in social organization ultimately depend on differences in the patterns of interactions among individuals. The dominance hierarchy and territoriality, two classical paradigms for social organization (see Schjelderup-Ebbe 1922, 1935; Howard 1920; Allee 1938, 1942; Nice 1941; Hinde 1956; Carpenter 1958), differ in the polarity in individuals' interactions. In a dominance hierarchy individuals are ranked by their success in competition for some resource or incentive, such as food or reproductive partners, and often by their success in agonistic encounters. Even when not directly interacting, individuals of different rank often adopt different postures or engage in certain behaviour patterns with different frequencies. Hierarchical organization of individuals thus involves two sorts of polarity in the social system: (a) interactions between individuals of different rank lack reciprocity; and (b) individuals of different rank differ in their behaviour even when not overtly interacting. To understand a hierarchical social organization, it is necessary to identify and characterize these polarities in the constituent individuals' relationships.

In contrast, reciprocity characterizes the relations of territorial individuals, a conclusion particularly evident when individuals restrict their activities to their own territories. In such species each individual inhabits his own territory, and neighbours meet as equals in agonistic encounters at their boundaries. Perhaps in most territorial species, however, individuals do not confine their movements to their own territories. A territory then emerges as an area within which the resident individual at any time can chase away an intruding individual or supplant the intruder at a food source. For example, within a limited area a nesting pair of bicolored antbirds *Gymnopithys bicolor* can supplant all other individuals from the choice feeding spots above swarms of army ants (Willis 1967); beyond this area the pair becomes subordinant to other individuals. In many species of birds, individuals maintain territories during the breeding season but during the winter range far beyond their former nesting territories. In a number of these species an individual's rank at a food source relates to the individual's distance from its previous or subsequent nesting territory (Brian 1949; Brown 1963; Dixon 1965; Hartzler 1970). Such observations have led several authors to define a territory as the area within which an individual successfully dominates agonistic encounters with other conspecific individuals and to define the boundary between neighbouring territories as the zone in which the dominance relationship between two territorial neighbours reverses (Tinbergen 1939; Emlen 1957; Willis 1967). Thus although hierarchical organization characterizes the interactions of territorial individuals at any one point in space, each territorial individual has some area in which it dominates all others. When their interactions are summed over large areas, individuals have reciprocal relationships.

This sort of hierarchy, in which dominance relations depend on location, is appropriately called territorial dominance. The term peck-dominance, which Allee (1942) applied to site-dependent dominance hierarchies, originally referred to hierarchies in which the outcomes of dyadic interactions were probabilistic rather than determinate (Masure & Allee 1934). Although most of the variability in the interactions within groups of pigeons, the 'type species' for peck-dominance, later appeared explained by the locations of interactions (Diebschlag 1941; Ritchey 1951; Castoro & Guhl 1958), the term peck-dominance is best restricted to its original meaning.

Territorial individuals might show a second sort of hierarchical organization, when certain areas are preferred for territorial occupancy. Territorial individuals in these circumstances would be ranked in accordance with the attractiveness of their locations, provided that territorial individuals in more desirable positions inhibited occupation of these areas by other territorial individuals established in less desirable positions. For this sort of hierarchical organization among territorial individuals, I shall use the term polarized territoriality.

Possibilities for this sort of polarity arise in most territorial species. Certain habitats are invariably more favourable for nesting, and these habitats presumably attract individuals establishing territories (for instance, Kluyver & Tinbergen 1953; Glass 1960; Delius 1965). Once the preferred areas are fully occupied, remaining individuals might either not establish territories, and thus constitute a non-territorial population of floaters, or they might establish territories in sub-optimal areas and subsequently move into better locations when opportunities arise. For several polygynous passerines that nest in marshes, differences in the vegetation in males' territories correlate with the number of mates the males can attract (Kluyver 1955; Verner 1964; Willson 1966; Verner & Engelsen 1970). In these species also, one might expect that individual males would relinquish their original territorial positions when vacancies arise, in order to relocate in positions that attract more females.

Available studies have seldom established that territorial individuals will move into more preferred positions. In a variety of birds, when territorial individuals are experimentally removed or disappear naturally, the vacated areas are indeed reoccupied fully or partially by newcomers (Stewart & Aldrich 1951; Hensley & Cope 1951; Orians 1961; Delius 1965; Holmes 1966; Bendell & Elliot 1967; Watson 1967; Harris 1970). In most of these studies, the previous status of the newcomers was unknown, so it is uncertain whether the replacements included floaters or territorial individuals or both. In his study of the red grouse *Lagopus lagopus scoticus*, Watson found that most new occupants had previously lacked territories. Some territorial individuals, however, did relinquish their original positions in order to establish new territories in the vacated areas, although Watson did not specify the qualities of their new territories in comparison with their former ones. When Harris (1970) removed oystercatchers *Haematopus ostralegus* from their territories, neighbouring territorial residents in less favourable habitats moved their territories into the openings. This finding that territorial individuals will relocate in response to adjoining vacancies in preferred areas provides indirect evidence for polarized relationships among territorial individuals.

Long-term investigations of territorial species have usually revealed that individuals' territories in successive years remain in nearly the same locations, results that suggest little polarity in the relationships of territorial individuals. This result has applied both to usually monogamous species like the song sparrow *Melospiza melodia* (Nice 1937; also see Lack 1943, and von Haartman 1949) and to the polygynous red-winged blackbird *Agelaius phoeniceus* (Nero 1956). Such studies, however, have not considered whether those shifts in territory location that do occur correlate with breeding success before and after the change.

Two possibilities could reduce the potential advantages of moving to a better location. Territorial individuals established in sub-optimal areas might fully or partially compensate for the inferior habitat by enlarging their territories. Furthermore, the value of a territory might improve with time, if familiarity with an area contributed substantially to an individual's breeding success there. In these circumstances, territorial individuals might not benefit from relocating and thus might fail to show any indications of polarity in their relationships.

To summarize, the relationships of territorial individuals, although reciprocal in many ways, can incorporate two sorts of polarity. Territorial dominance occurs when individuals' interactions at any one site conform to a site-specific dominance hierarchy but when summed over large areas show reciprocity. Territorial dominance probably occurs in all territorial species, although it is most evident when individuals regularly visit each other's territories. Polarized territoriality, in contrast, involves a hierarchical organization of territorial individuals according to the locations of their territories. Polarized territoriality will develop when some territorial individuals occupy preferred areas and prevent other territorial individuals from establishing themselves in these areas. In these circumstances, the interactions of territorial individuals even when summed over large areas will reveal certain polarized relationships.

B. Prospectus

This paper will suggest that the interactions of male sage grouse include both reciprocal and non-reciprocal features and do not exactly fit the classical conceptions of either territoriality or dominance hierarchies. Instead, the model of polarized territoriality best explains the behavioural regulation of their mating system. Fully adult male sage grouse occupy nearly exclusive territories on their communal display grounds. However, since females congregate for mating at particular sites within a lek, the locations of territories differ in the opportunities they present for mating. Polarity in the territorial behaviour of males involves both: (a) differences in the behaviour of territorial males established at different distances from a mating centre, and (b) non-reciprocal interactions of territorial neighbours at their mutual boundaries. In particular, males move their territories in order to occupy vacancies that arise nearer a mating centre.

III. OUTLINE OF THE LEK BEHAVIOUR OF SAGE GROUSE

Sage grouse reach greatest abundance on the sagebrush prairies of the high intermontane basins from Montana and Colorado west to Washington and north-eastern California. The species depends for food and shelter primarily on one plant, the big sagebrush *Artemisia tridentata*, an evergreen shrub. During winter large flocks wander over the prairie, where they seek areas free of deep snow. As the weather improves during February and March, males begin to visit their communal display grounds (leks). The total number of males attending each lek ranges from only a few to over four hundred (Patterson 1952). On large leks the males spread over a hectare or more. Each lek recurs from year to year at a traditional site on the prairie (Section VI).

Males usually attend their leks early each morning, and often in the evening and all night, from February or March into May. Females arrive for mating primarily during several weeks in late March or April (Scott 1942; Batterson & Morse 1948; Patterson 1952; Dalke et al. 1960, 1963; Eng 1963). My records at the Fords Creek Lek in Montana in 1968 (Fig. 1) conform to the seasonal pattern reported by these other observers. Visits by females rapidly reached peak numbers in the last few days of March, then decreased gradually over 3 weeks. Unusually low counts of females occurred on mornings when there were strong winds or when fresh snow covered the ground. Almost all copulations came within a 3-week period.

A brief sketch of the activity on a sage grouse lek during a typical morning in the mating period will help in understanding the following sections. Many of the points introduced here will receive full treatment later.

On moonlit nights activity may continue all night but usually reaches a peak about sunrise, when females are most numerous. On a typical morning during the height of the mating period, activity increases during the hour before sunrise. Males not already present on their territories arrive at least 1 hr before sunrise. The males occupy small, contiguous territories, 13 to 100 m² in area; each male occupies the same territory every day. Within his territory a male

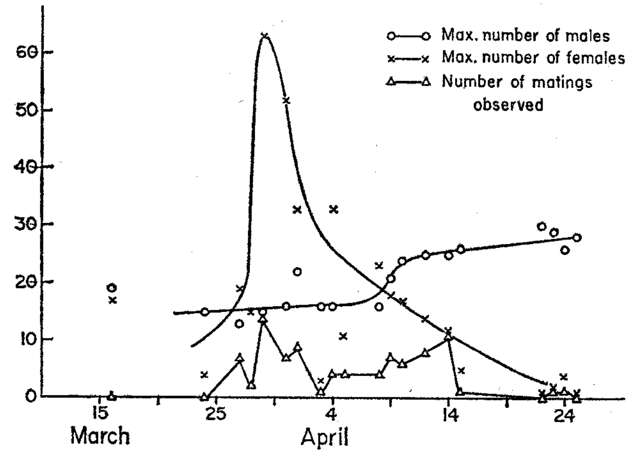


Fig. 1. Seasonal changes in the numbers of males, females, and matings on the Fords Creek Lek, 1968. The numbers of males and females are the maxima present at any one time each morning.

assumes the 'strutting posture' (Plate II, Fig. 4), with his tail cocked and fanned, his head raised, and the white feathers and black plumes on the sides of his neck erected.

At intervals of 7 to 10 s each male performs an elaborate, stereotyped display, called a 'strut'. By a complex sequence of motions, the male inflates a large expansion of his oesophagous (Plate II, Fig. 3) and then deflates it suddenly to produce a plosive sound with a peculiar resonant quality. From time to time two males on neighbouring territories interrupt their strutting to confront each other at their territorial boundary in a 'facing-past encounter'. In these encounters the males do not face each other head on; instead, they take positions shoulder to shoulder, so that each faces past his opponent's side (Plate II, Fig. 7). In high-intensity encounters the males close until they are side-by-side, several centimetres apart, facing opposite directions. An encounter usually involves some manoeuvring backwards and forwards for position. Either opponent will dart forward several centimetres and force his opponent to retreat. Their roles switch quickly, each male retreating as his opponent advances, so the contestants rarely move more than ½ m backwards and forwards. An encounter often erupts into fighting with the wings. Although each male strikes his opponent vigorously, I never saw a male injured or forced to move his territorial boundary as a result of these encounters. At most, a few contour feathers or under-tail-coverts were lost.

Just before sunrise the smaller and drably coloured females begin to arrive in large numbers. On moonlit nights some females are present on the lek at all times during the night. Females also visit the leks in the late afternoon during the males' evening display period, but they are much fewer in the evening than at dawn. The females congregate in dense packs for mating only at particular sites in the lek, the mating centres (Scott 1942) (Plate I, Fig. 2). Every morning during the mating period females gather in the same limited areas, which are roughly 5 m in diameter, although the surrounding territorial males spread over a hectare or more. During the height of the mating period each female usually arrives alone or with one or a few other females (Section VIII, A). They fly directly across the lek, above the strutting males, and land near the far edge of the lek. A female then frequently walks directly to the nearest mating centre, detouring only slightly to avoid peripheral males strutting in her path, or occasionally pausing briefly. When she reaches the mating centre she joins the gathering pack of females there.

That male whose territory includes the mating centre performs most of the copulations at the mating centre (Section VII). One male mated with more than thirty females in 3 hr. Females congregated at a mating centre adopt a posture with their heads withdrawn onto their shoulders. Although they stand only several centimetres apart in these dense congregations, the females interact with each other remarkably little. Each steps out of the path of a moving bird and moves enough to avoid close approaches by the strutting male. Before copulation a female assumes the 'solicitation posture', crouched with wings spread and neck extended. A female usually copulates only once each season and lays her clutch of six to eight eggs after leaving the lek.

Some females probably travel a number of miles from the lek at which they mated before they nest (Dalke et al. 1963; Patterson 1952). Each female builds her nest on the ground and cares for her eggs and young with no co-operation at all from a male.

IV. BEHAVIOUR PATTERNS OF SAGE GROUSE

Lumsden (1968) and Hjorth (1970) have described the behaviour patterns of both sexes of sage grouse. For the purposes of this paper, brief summaries of their observations, amplified where necessary by my own, will suffice. Since I do not always concur with the internal states or communicatory functions that Lumsden ascribes to behaviour patterns, I have changed Lumsden's terminology when it suggests an uncertain interpretation of the animal's internal state or the communicatory function of the behaviour. I have substituted more descriptive terms, that suggest the bird's stance, movements, sounds, or feather erection.

A. Male Behaviour Patterns

Facing-past encounter. This is an encounter between two neighbouring territorial males usually within the boundary zone between their territories. The two males take positions either shoulder-to-shoulder, so each faces past the other's side (Plate II, Fig. 7), or side-by-side. Often the two opponents jockey for position tensely, each alternately advancing and retreating a few steps. Bouts of a harsh, stacatto vocalization, 'gutteral vocalization', accompany these encounters.

Wing-fighting. Overt fighting in which two contestants side-by-side beat each other vigorously with their wings. No serious injury was ever recorded. Wing-fighting usually occurs in brief bouts lasting 1 to 10 s.

Strutting posture. A posture assumed by males before and after bouts of strutting and between struts within a bout. The male stands with his body tilted upward and his head held high (Plate II, Fig. 4). He cocks and spreads his tail, erects the white feathers and thin plumes on the sides of his neck, and expands the yellowish combs over his eyes.

Strut. An elaborate display regularly performed by males within their territories. Strutting occurs both when females are present on the lek and when they are absent, although it is more persistent in the former situation. The strut display features the breeding male's inflatable chest sac, actually a large (4 to 5·5 litres; Clarke, Rahn & Martin 1942) expansion of the oesophagus. This oesophageal sac enlarges during the breeding season, and the overlying skin of the chest becomes edematous and vascularized (Clarke et al. 1942). Starting from the strutting posture, the male twice raises this chest sac as high as possible and drops it. Each time before lifting the sac the male extends his wings forward and then, as the sac rises, pulls them backwards across the specialized, stiff feathers on the sides of his chest (Plate II, Fig. 3). Thus each time the chest sac rises, the wings produce a swishing sound against the sides of the chest. As the sac is raised and dropped, it fills with air and extends. As a result, two bare, yellowish olive patches of skin expand on the male's chest. After the sac falls the second time, it is compressed by the contraction of superficial muscles in the skin of the chest. Immediately after compression, the air in the sac is released into the bare patches of skin, which suddenly balloon forward and then instantly collapse. As the bare skin patches distend and collapse, two sharp snaps are produced approximately 0·1 s apart. A peculiar resonant quality accompanies the snaps, and several brief, soft coos precede them. Thus, the entire acoustic output from the display is 'swish–swish–coo-oo-poink'. Following a strut the male returns to strutting posture. The display itself lasts slightly more than 2 s. A male usually struts at intervals of 7 to 10 s; intervals of 5 to 6 s are rare. The sounds of the males strutting on a lek can usually only be heard within several hundred metres of the lek. In contrast, the males' white chests, which bob up and down during their displays, are conspicuous more than 1 km away.

Sleeked, relaxed, and semi-relaxed postures. The postures of male sage grouse grade continuously from the strutting posture to the 'sleeked posture'. In the sleeked posture the male stretches his neck upward, closes his tail and holds it slightly below horizontal, and sleeks his neck feathers. Sleeked posture occurs during wing-fighting and also when the male is alarmed by an approaching predator or a man. The 'relaxed posture' differs from the sleeked posture in that the feathers of the neck and body are relaxed instead of sleeked (Morris 1955) and the head is not extended (Plate II, Fig. 6). Males assume this posture late in the morning before leaving the lek and also during wing-fighting as an intermediate between sleeked postures and 'semi-relaxed postures'. In semi-relaxed posture (Plate II, Fig. 5), the male still keeps his tail folded and roughly horizontal, but the white feathers and thin plumes on the sides of his neck are erected, and his eye combs have usually partially expanded. This posture is frequent in facing-past encounters and also during long intervals between bouts of strutting. Since in both situations it may continue for minutes at a time, the semi-relaxed posture represents a prominent mode in the continuum between relaxed and strutting postures. Other intermediates are transitory. In the continuum from relaxed to strutting posture, components of the strutting posture are usually added in an orderly sequence: (1) neck feathers erected, (2) tail fanned and cocked, (3) head raised and body tilted. Some variations in this sequence occassionally occur, though. In facing-past encounters the elevation of the tail varies considerably. A male sometimes partly cocks his tail for brief periods even though his neck feathers are relaxed. The eye combs expand maximally in strutting posture and collapse during sleeked posture. In intermediate postures the expansion of the eye combs varies.

B. Female Behaviour Patterns

Solicitation posture. The posture adopted by females prior to copulation. The female crouches and arches her wings by raising her carpal joints while fanning her primaries to the ground.

Copulation. The female in solicitation posture is mounted by the male. The male usually spreads his wings to the ground on either side of the female in order to retain his balance, treads her back with his feet, and then lowers his tail with a rotatory motion which results in cloacal contact. The entire procedure lasts 5 to 10 s.

Post-copulatory ruffling. After only a second or two of cloacal contact, the female dashes forth from under the male. The male is left squatting on the ground, his wings still sprawled to either side. After a pause of 5 to 10 s he resumes strutting. The female, as she dashes forward, begins vigorous shaking movements. She rapidly opens and closes her tail, fluffs all her feather tracts, and shakes her partly opened wings up and down alternately. This behaviour apparently only follows completed copulations (Section VII, B). In other situations females occasionally shake themselves briefly, but after a completed copulation a female will continue post-copulatory ruffling for 10 to 15 s and even sporadically thereafter. As the ruffling subsides, the female begins prolonged periods of preening, which often last 15 min or more.

Quacking call. A harsh, single call uttered by flying females. The tonal quality suggests the quacking of a female mallard. These calls are particularly frequent as the females fly over the lek on arrival at dawn. However, as Lumsden also noticed, they sometimes are heard when females take flight later in the morning to leave the lek (Section VIII, A).

V. TERMINOLOGY, STUDY SITES, AND PROCEDURES

A. Definitions

Lek. An aggregation of individuals at a traditional site for mating, but not for parental care or nesting. By extension, the site itself is often called a lek, although some authors have used 'arena' or 'communal display ground' instead. Originally a Scandinavian term meaning play or courtship antics (Swedish and Norwegian lek, Danish leg), lek is now regularly used in the ornithological literature in other languages.

Polygamy. An unbalanced sex ratio among breeding individuals, regardless of how long mated individuals associate. Polygamy has often meant, to ornithologists, that individuals of one sex form durable bonds with two or more individuals of the other sex (for instance, von Haartman 1951; Lack 1968). Promiscuity has referred to the absence of stable pair-bonds between breeding individuals of opposite sex. These usages confuse two separate features of a mating system: the length of time that mated individuals associate with each other, in other words the duration of the pair-bond; and the sex ratio among breeding individuals. In the present paper polygamy means that more individuals of one sex contribute gametes in any breeding season than do individuals of the other sex. Polygyny specifies that fewer individual males than females contribute gametes; polyandry the converse. Thus, in these definitions, the duration of the pair-bond has no necessary connection with the breeding sex ratio.

Yearling. A bird approximately 1 year old. Since the eggs of this species usually hatch in June, during the subsequent breeding cycle (March to August) yearlings are 8 to 14 months old.

B. Study Sites

In order to observe leks with different numbers of attending males, I studied three leks in three seasons of field work. In 1967 I worked at the Muddy Springs Lek, Albany County, Wyoming (33 km north of Laramie, Wyoming; 41° 32′ 30″ N, 105° 34′ 40″ W; R. 73 W, T. 18 N, section 9; elevation 7200 feet), the same lek that Scott (1942) had observed in 1940 and 1941. Work continued from 10 April until 25 April. In 1968 I worked at the Fords Creek Lek, Fergus County, Montana (5 km north-north-west of Grass Range, Montana; 47° 08′ 15″ N, 108° 52′ 05″ W; R. 22 E, T. 16 N, section 24; elevation 3550 feet), the lek that Lumsden (1968) had observed in 1965. Observations here continued from 16 March until 25 April. I arrived in time to observe the lek briefly before mating began on 27 March. In 1969 I made an attempt to begin studies at a large lek well before mating began. However, an unseasonal snow-storm made travel over the prairie impossible until 31 March, once again shortly before mating began. The lek studied was Dry Sandy Lek No. 1, Sweetwater County, Wyoming (21 km north-east of Farson, Wyoming; 42° 13′ 55″ N, 109° 14′ 40″ W; R. 104 W, T. 26 N, section 17; elevation 6810 feet). This lek was located by Patterson in 1949 (Patterson 1952: Fig. 4, lek No. 31). After observations began on 31 March, they continued until 28 April.

C. Observation Procedures

Each year on arrival I erected a blind (hide) with a clear view of one mating centre. Subsequently, apart from minor adjustments, I did not move my blind, in hopes of encouraging the grouse to habituate to its presence. This procedure seemed successful, since in each year both males and females regularly walked calmly within a few metres of my blind. However, as I shall describe below, my blinds may have caused some disturbances soon after they were erected in 1967 and 1968.

In 1967 observations were made in the evenings, beginning before the males arrived on the lek and continuing until dark. However, most of my observations that year and almost all observations in 1968 and 1969 were made during early morning. My usual procedure was to arrive at the lek at least 1 hr before sunrise (03.45 to 05.00 hours MST, depending on the time of sunrise), soon after the first light in the east on dark nights. I quickly transferred my equipment to my blind and then continued observations until the males had left for the morning, usually between 08.00 and 09.00 hours. On nights with a full moon in the morning hours I usually flushed the males near my blind as I entered it, since males often remained on the lek all night when the moon was full (see Patterson 1952). Most males seemed to return and resume activity within 15 min of my entering the blind. On moonlit nights females also visited the leks. When the birds flushed as I entered my blind on these nights I sometimes heard the distinctive quacking calls of some flying females. On dark nights with a new moon I usually found no birds on the lek when I arrived. Even if females regularly visit the leks on moonlit nights, most still arrive around sunrise (Section VIII, A).

D. Counts of Birds

The maximum numbers of males counted at one time on each of the leks were respectively 154 (20 April 1967), 30 (22 April 1968), and 260 (24 April 1969). The number of males that displayed at a lek varied somewhat from day to day, especially in late April when many yearlings were present. The maximum number of 260 for 1969 is too low, because I could not quite see the entire lek from my blind. I probably missed between 10 and 20 males.

Accurate counts of the numbers of females were even more difficult to obtain, because of the large areas covered by the leks in 1967 and 1969 and the inconspicuousness of the drab females among the sagebrush. In 1969 I made special efforts to get counts of females at different times during the morning on several days.

E. Recognition of Individuals and Age-Classes

To minimize disturbance of the birds' behaviour I did not capture grouse on their leks in order to mark them. Instead, I discovered that I could recognize individual males and separate yearling and older males without handling the birds. I was not, however, able to detect individual differences among the females.

Individual differences among males were found in the numbers of rectrices and the patterns produced by the white tips of the under-tail-coverts. In the strutting posture a male cocks his tail vertically and fans it, so that seen from the rear the white tips to his under tail-coverts form a bold pattern of white spots. Soon after beginning field work in 1968 I realized that these patterns of spots could identify many individual males throughout a season. In 1968 and 1969 most males under-tail-coverts were photographed at intervals of a week or more throughout the duration of my observations. Plate III, Fig. 8 shows the distinctive patterns of four typical males in 1969. During my observations in 1967 I had to rely solely on the site-constancy of the males near my blind to identify them. However, by examining the films taken at intervals throughout that season, I could confirm by their under-tail-covert patterns the identities of six males around the mating centre. The patterns remained reliably identifiable in spite of periodic disturbance to the feathers by wind or changes in a bird's posture.

Major changes in these patterns seemed to occur only when a male lost under-tail-covert feathers, so that a gap appeared in his previous pattern. In 1969 I observed a facing-past encounter in which male 9 lost about three of his under-tail-coverts in a fight. I recorded before and after the encounter the pattern of his white spots. In 1968 male N's under-tail-coverts pattern changed by the deletion of several feathers. Although I did not see the fight that I presume was responsible for the deletion, everything indicated that the same individual was involved before and after the change.

Further confirmation of a male's individual identification came from the number of his rectrices. Most males had either nine or ten tail feathers on each side; a few had nine on one side and ten on the other. I had difficulty counting the tail feathers of males that were more than

30 m from my blind, but the numbers of rectrices of all closer males were recorded several times during the season. Occasionally I could identify an individual male by other peculiarities. For example, male B in 1968 had an unusually white throat; male TM in 1968 and males 10 and 12 in 1969 had lost or broken one or more of their tail feathers.

Maps 1, 3 and 11a present the locations of individually identified males in 1967, 1968 and 1969. I have also indicated positions regularly occupied by males that I did not identify individually.

Sage grouse like other grouse retain their outer two juvenile primaries during their first year of life, so yearling sage grouse can be reliably identified in the hand (Petrides 1942; Patterson 1952; Eng 1955). Other characteristics of yearling males are reviewed by Patterson (1952: 128, 153–4) and briefly by Eng (1963). They mention the yearlings' shorter, blunter rectrices, smaller chest sacs and a brownish zone across the lower chest, which in older males is white. The first distinction was the easiest for me to observe in the field. Few males had tail feathers intermediate between the long, tapering tips of the older males and the blunter tips of the yearling males. Furthermore, tail feathers of yearling males were often of irregular length. Other characteristics became less noticeable as the season advanced, as Eng (1963) also noted. For instance, in late March and early April occasional males with noticeably smaller chest sacs and brownish lower chests would strut erratically around the periphery of a lek. However, by late April even males with very stubby tail feathers often had apparently full-sized chest sacs and lacked obvious differences in the colouration of their chests. Since other aspects of the yearling males' morphology appeared to change as the season advanced, I based my identification of yearlings upon their comparatively stubby tail feathers.

Dalke et al. (1963) suggest that some yearling males become indistinguishable in the field from older males, but the evidence they present is incomplete. They report that some males with 'full adult plumage' were identified in the hand as yearlings by their retention of two outer juvenile primaries. It is not clear from their statement, however, whether they based their judgment of 'full adult plumage' only on the size of the chest sac and the colour of the chest, or whether some yearlings grow tail feathers resembling those of older males. I encountered few males (ST in 1968, SE in 1967) that were difficult to place either as yearlings or older males on the basis of their tail feathers. Even if a few yearling males do grow long-tapering rectrices, it seems likely that all males with blunter rectrices are yearlings.

F. Records of Matings

Each year for every mating observed or filmed at the mating centre under study, I recorded the male that performed the copulation, his location on the lek, and whether or not the copulation was interrupted by another male. I did not record matings at other mating centres within the same lek. Furthermore, I missed many of the matings in the areas I studied, including all those that occurred during the evenings, at night, and on the occasional mornings when I did not observe the lek. I also undoubtedly overlooked some matings that occurred during my observation periods.

Copulations probably occurred infrequently on moonlit nights and not at all on other nights. On every morning of my observations on which females were numerous, the females began arriving in large numbers, roughly 1 hr after I had entered my blind (Sections V, C and VIII, A). Scott's (1942) all-night observations confirm my impression that mating was infrequent at night.

The pertinent question is whether I tended to overlook the matings of peripheral males more than those of males in the mating centre. Certainly, many of the peripheral males were farther from my blind and thus more difficult to observe. On the other hand, on days of peak mating the one or two males in the centre of the pack of females often copulated so frequently that I must have missed some of their matings. It is impossible to assess how these counteracting biases might have affected my data on the distribution of matings among different males. My impression is that, if anything, I underestimated the proportion of matings performed by the few very successful males.

G. Records of Spatial Relationships

To help in locating birds on the lek, I placed small flags in a 15·4-m grid over the area under study. Each flag was made of a few short pieces of surveyor's marking tape tied to the end of a metre length of heavy wire. The birds appeared to ignore these markers. As a further aid in locating positions on the lek, I prepared base maps on which all salient clumps of sagebrush were indicated. I judged that my inaccuracies in locating a bird's position were probably no more than ½ m. However, birds over 50 m from my blind were more difficult to locate, and their positions probably included greater inaccuracies, especially in the radial direction from my blind.

I frequently mapped the birds' positions and recorded their movements in field notebooks. However, most of my data on the positions of matings and facing-past encounters come from time-lapse films. I contrived a method for advancing a Bolex H16 movie camera one frame at a time by means of a solenoid regulated by a timing module. On twenty-nine mornings in 1968 and 1969 I recorded birds' activities on time-lapse film for between 1 and 2½ hr. The field of view usually included five to ten territorial males at various distances from a mating centre. In 1968 I used a filming speed of one frame every 3 to 4 s; in 1969 I filmed at about 1 frame per s. On each morning I determined the precise rate with a stopwatch. Since males strutted every 6 to 10 s and remained in one position between struts, except when they were engaged in mating or in a facing-past encounter, I could record virtually all the males' behaviour by using these filming speeds. Movements of females were also slow enough that they could usually be followed in my time-lapse sequences. Using Kodak Tri-X film (ASA 200), I could usually begin filming shortly before sunrise.

Thus, in 1968 and 1969 I could record the positions of large numbers of facing-past encounters between neighbouring males and the positions of many matings. Since most of the positions I recorded were taken from my time-lapse films, emphasis is placed on the few males that I usually included in the camera frame. In each year the territories of males near one mating centre were well documented by time-lapse films. Territories of more perhipheral males extended 10 to 15 m in all directions beyond these well documented areas.

The resulting maps are placed together at the end of this paper so that they can be compared easily. In some of the maps I have plotted the positions of facing-past encounters and placed numerals or letters identifying individual males near the centres of their territories. Each such plot is interpreted in the immediately preceding map, in which I have drawn territorial boundaries (thick lines) based on the facing-past encounters. In zones where no facing-past encounters were recorded, I have estimated territorial boundaries on the basis of the males' movements (thin lines). Notice that linear boundaries represent a considerable abstraction of the facts, although they do promote clarity in the maps. In reality, territorial boundaries between male sage grouse are zones of varying width in which facing-past encounters concentrate: a point to which I shall return.

H. Samples of Male Activity

The time-lapse films were also used to sample the males' activities during 6-min periods. I wanted to compare the activities of males successful in mating with those not so successful and of yearling males with older males and to assess the effect of proximity to females on the males' activities. To compare successful and unsuccessful males at the height of the mating season, I chose twenty-eight 6-min sequences of time-lapse film from 27, 29 and 31 March and 1 and 3 April 1968. All sequences were separated by at least 5 min. Each male in each 6-min period was classified according to his proximity to females. Three situations were recognized: (a) a female or females within his territory (situation T); (b) a female or females within 10 m of the male in a neighbouring territory but not in his own territory (situation N); and (c) no females within 10 m (situation O) during the 6-min period. Thus the behaviour of individual males could be compared under conditions of roughly equivalent proximity to females. Eight males appeared in eight or more of the twenty-eight 6-min samples: Male D in twenty-eight samples; male B in twenty-seven; male X in twenty-two; males TM and UT in nineteen each; male A in eighteen; male C in ten; and male CN in eight samples.

In each 6-min period I counted how many times each male in view during the entire period strutted. In addition, in every third frame (about every 12 s) I recorded whether the male was in strutting posture, in semi-relaxed posture, in relaxed posture, in a facing-past encounter, mating, or chasing an intruding male (see Section IX, J). Thus, for each male in each sample I could estimate the total amount of time spent in strutting posture and in facing-past encounters and the total number of struts during the period. For example, the proportion of time spent in strutting posture was estimated by dividing the number of sampled frames in which the male appeared in strutting posture by the total number of sampled frames in the 6-min period. The proportion of time in facing-past encounters was calculated in the same way.

I also recorded the number of facing-past encounters in which each male participated during each 6-min period. The duration of each facing-past encounter was estimated by dividing the number of sampled frames in which it appeared by the number of seconds between sampled frames (about 12 s, varying slightly as my filming rate changed). These estimates are not reliable for very long nor very short facing-past encounters. Brief encounters, which did not appear in a sampled frame (recall that I sampled every third frame), were treated as if they had appeared in one sampled frame. In other words, they were assigned a duration of roughly 12 s. It is unlikely that any encounters were so brief that they would not appear in at least one frame. So I overestimated the lengths of very short facing-past encounters. When the beginning or end of an encounter was not included in a 6-min period, I doubled the duration of the encounter within the 6-min period. For example, an encounter that appeared in the first ten sampled frames was assigned a length of twenty sampled frames. On the average the limits of my 6-min periods should have fallen randomly on either side of the midpoints of these encounters. Encounters that persisted throughout an entire 6-min period were arbitrarily assigned durations of 6 min, so I underestimated the lengths of very long encounters. Since most very short encounters occurred among males with females inside their territories (situation T) and most very long encounters involved males with no females nearby (situation O), my errors in estimating the durations of facing-past encounters would tend to underestimate differences between males in these two situations (see Section VIII, B).

In order to compare the behaviour of older and yearling males I employed the same procedure in taking eight 6-min samples from time-lapse films exposed on 22, 23 and 25 April 1968. Nine adult males appeared in these samples (D, B, A, UT, X, N, F and H) and four yearling males (K, Z, J and Y).

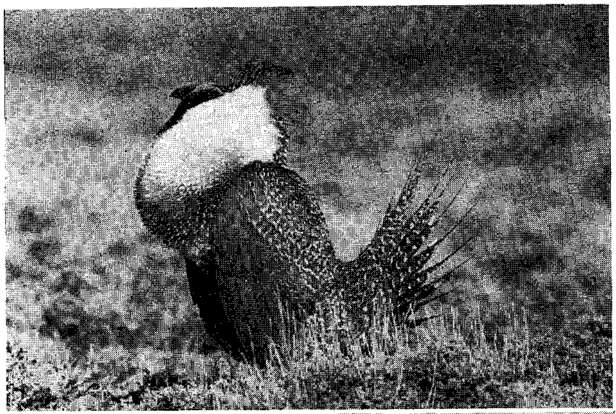
I. Samples of Female Activity

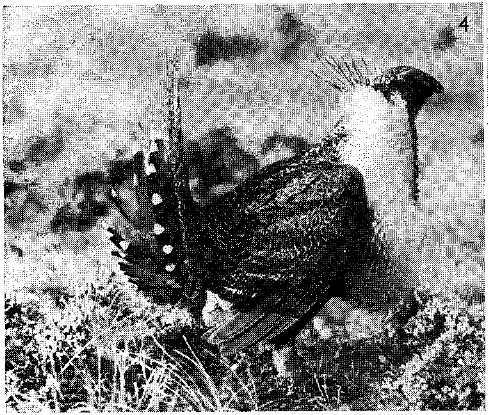
In 1969 I undertook systematic observations to estimate the incidence of certain female activities during the course of the morning. On 11, 14, 16, 17 and 18 April at intervals of 15 min or more, I scanned the lek with binoculars and classified the behaviour of every female I saw. After a little practice this procedure took about 5 min. These surveys included only about half of the lek, an area containing two mating centres.

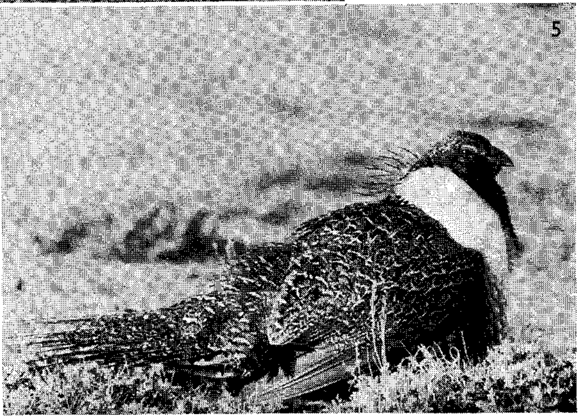
PLATE I

Fig. 2. View of mating centre no. 3, Dry Sandy Lek, 1969. Territorial males occupy positions around the dense aggregation of females at the mating centre in the middle of the photograph. Mating Centre no. 2 appears in the right background.

PLATE II







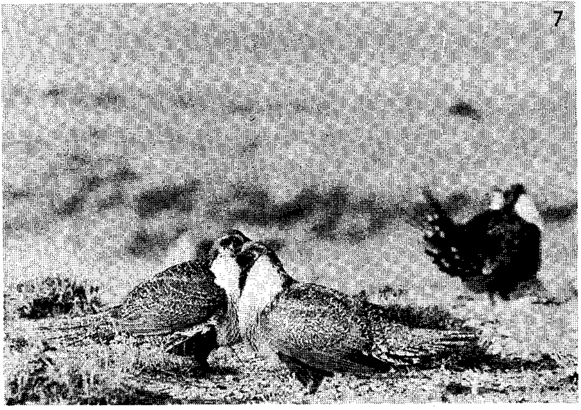


Fig. 3. Strut. As the chest sac is lifted, the wings scrape the sides of the chest.

Fig. 4. Strutting posture.

Fig. 5. Semi-relaxed posture.

Fig. 6. Relaxed posture.

Fig. 7. Facing-past encounter.

PLATE III

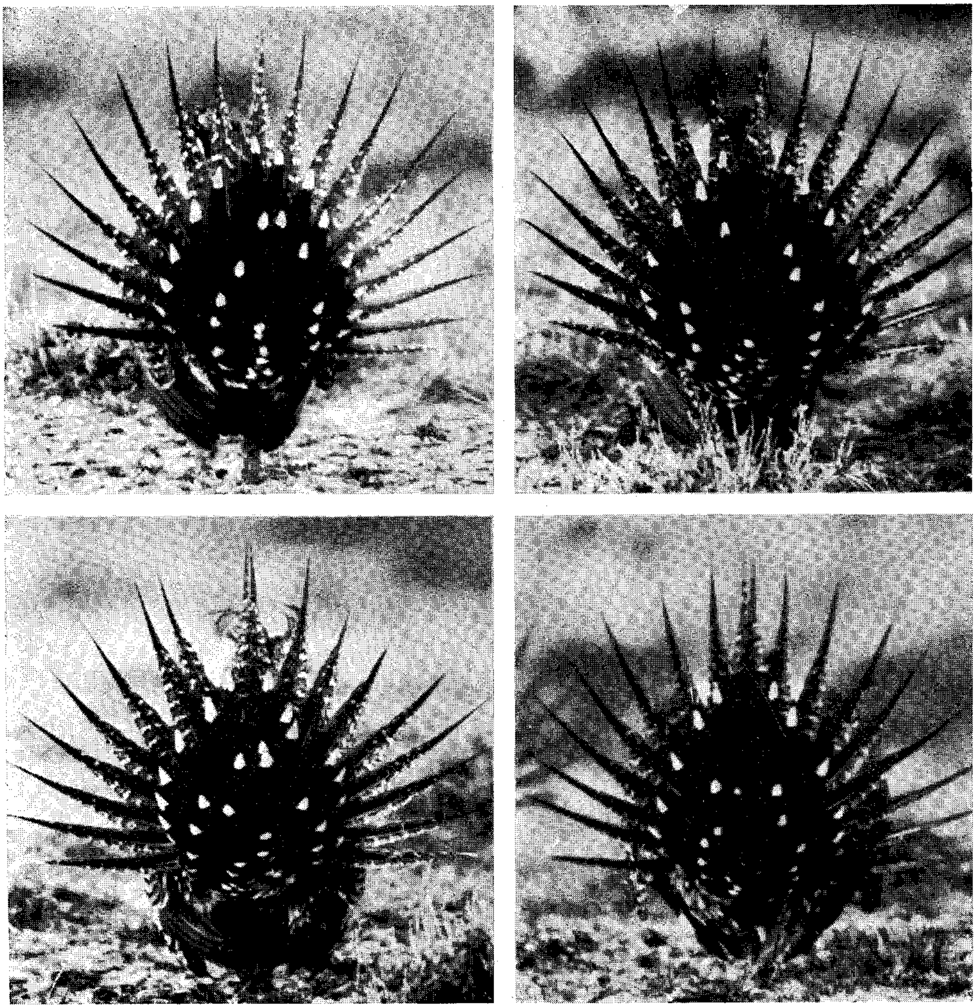


Fig. 8. Rear views of four males in strutting posture, Dry Sandy Lek, April 1969. Upper left: male 3. Upper right: male 13. Lower left: male 7. Lower right: male 4.

I counted the number of females at each mating centre. Those females not at mating centres were classified as either walking or pausing. For each walking female I recorded whether she was walking toward (±30 degrees) the nearest mating centre or not. For each pausing female I recorded whether or not she was within 3 m of a male, whether or not she was within 3 m of another female, and whether or not she was feeding or preening. Twenty-three such surveys were completed. However, in two of the surveys I recorded fewer than twenty females, which probably does not constitute an adequate sample for estimating females' activities. On 16 April ten surveys were completed, of which nine included more than twenty females.

VI. TRADITION IN THE LOCATION OF LEKS AND MATING CENTRES

A. Size and Traditional Location of Leks

Sage grouse leks differ from lek to lek in the number of males attending them, but regardless of its size a lek usually recurs from year to year at the same site. For three years, 1949 to 1951, Patterson (1952) censused all the leks on 250 square miles (647 ha) of sagebrush prairie in the Green River Basin in western Wyoming. Every lek that he located in 1949 recurred in the same locations in both succeeding years, and no new locations were found. In 1949 the number of males per lek averaged seventy-one, although the number of males on different leks varied from six to 400. In 1949 the median number of males per lek was fifty-eight. Four leks that year included more than 125 males. The forty-four leks represented an average of one to every 5·7 square miles (14·7 ha).

The Muddy Springs Lek near Laramie, Wyoming, provides striking evidence of the traditional location of a lek. Scott (1942) studied this lek in 1940 and 1941, and 28 years later when I studied this same lek in 1967 its location had not changed. However, the maximum number of males attending the lek had dropped from 355 to 154. The lek I studied in 1969, Dry Sandy no. 1, Patterson had located and censused at the same spot in 1949 (Patterson 1952: Fig. 4, lek no. 31). From 1949 to 1951 the number of males fell from 183 to 167, while in 1969 the maximum was over 260. Occasionally old leks do disappear and new ones form as the populations of sage grouse fluctuate from year to year. Usually these changes involve leks with only a few males (Batterson & Morse 1948; Dalke et al. 1963). Thus, although leks show considerable variability in the number of males attending them, all except some of the smallest ones tend to recur from year to year at the same locations on the prairie.

Although the clustering of displaying male sage grouse at particular sites on the prairie cannot arise from any limitation of suitable locations, the leks tend to occur in places with certain common features (Patterson 1952; Lumsden 1968). Many leks, including the ones I studied in 1967 and 1969, occur beside intermittent streams between rises in the surface of the land at least $\frac{1}{2}$ km away in either direction. The lek I studied in 1968 was also in such a shallow valley. For a bird like the sage grouse, whose eye-level is no more than $\frac{1}{2}$ m above the ground, a broad valley might offer advantages in detecting approaching predators. The bird would have a clear view of the ground as far as the nearest rises in the prairie, often $\frac{1}{2}$ km or more in all directions. A position on top of a rise, in contrast, would leave the adjacent low-lying areas obscured by sagebrush near the bird. Leks also usually occurred in areas where the sagebrush was sparser and grass or bare soil covered more of the ground. Such areas probably allowed the males greater freedom of movement.

Even within a lek displaying males preferred areas with certain features over other areas. Here again these preferences cannot entirely explain the spatial relationships of the males. In Petroleum and Fergus Counties, Montana, leks tended to occur in areas where the sod-forming short grass *Bouteloua gracilis* covered much of the ground. Territorial males on the Fords Creek Lek preferred to strut on patches of this grass and avoided adjacent patches of bare ground a few centimetres lower in level. A sod-forming short grass also covered much of the Muddy Springs Lek, which I studied in 1967. Mats of sod were interspersed with patches of a grass that did not form sod and that grew on slightly lower ground. The displaying grouse preferred to use the carpet-like mats of sod. In 1969 little grass grew on the lek I studied. Here the males preferred areas where the sage grew more sparsely.

Some selection of sites for display therefore occurs on both a large scale and a small scale. On a large scale, the leks appear selectively in areas where shrubby vegetation is more widely dispersed. On a small scale, the displaying males chose slightly elevated mats of sod. Both preferences undoubtedly increased the displaying males' conspicuousness and freedom of movement. However, these preferences cannot completely explain the aggregation of the displaying males. The clustering of males into leks clearly exceeds the patchiness of the distribution of openings in the sagebrush. Similarly, within a lek the distribution and sizes of mats of sod do not entirely explain the locations of males' territorial boundaries (Section IX, B).

B. Traditional Location of Mating Centres

Mating centres, like the leks themselves, often recur from year to year in the same or nearly the same sites. Scott (1942) remarked that five mating centres in the large lek he studied occupied at least approximately the same sites in both years of his study. Patterson (1952, p. 158) also mentions that packs of females gathered at the same spots within a lek in successive seasons. On two of the leks that I studied the mating centres occupied similar positions in two years. The Dry Sandy Lek had four mating centres in 1969. When I visited the lek on 30 April of the preceding year two of those mating centers were in at least roughly the same positions. Since very few females were seen on that date late in the season, I had to base my judgment on the fact that territorial males cluster more densely around mating centres, information that only approximately specifies the position of a mating centre (see Section VIII, C). The mating centre that I studied on the Muddy Springs Lek in 1967 was located in precisely the same spot in 1968. Its location, determined on 3 May 1968, was immediately apparent, since the packs of females that had gathered there had trampled the grass to its roots, as they had done in the preceding year.

In two years I recorded changes of 8 to 15 m in the positions of mating centres. In both these years it seemed that my own activities nearby influenced these shifts. In 1967 I began observations on 10 April when females were already numerous on the Muddy Springs Lek. I erected my blind that day without knowing the exact location of the mating centre. It turned out that I probably set it within 10 m of the mating centre. The following morning as many as forty females gathered around one male (male A) at a spot 15 m north of my blind (northern site; n, Map 1). However, that evening I watched male A twice move about 10 m south-west and begin to strut in an area about 10 m north-west of my blind (Map 1). He encountered a neighbouring male at the edge of this area. Also one female solicited for copulation at this south-west site. The following morning, 12 April, the females at first congregated even farther from my blind, 30 m to the north, but after about 15 min they dispersed and gathered again around male A, 15 m north of my blind. It snowed most of that afternoon, so the following morning, 13 April, very few females appeared on the lek. Some of these visited the area 15 m north and others the area 10 m north-west of my blind. On the morning of 14 April, when activity once again reached high levels, females showed no interest in the area 15 m north of my blind, and as many as forty-two congregated in the area 10 m south-west instead. Male A never left this area all morning and copulated over thirty times. On subsequent mornings females always congregated at this place and never again revealed any interest in the site north of my blind. This south-western site 1 year later showed clear signs that the packs of females had gathered there in 1968 also. I believe that by placing my blind so close to the south-western site I may have temporarily influenced the females to gather farther away. On this same lek Scott (1942) observed one mating centre in 1941 that moved temporarily after a snow-drift had covered its original location.

The situation in 1968 was more confusing. The Fords Creek Lek included many fewer males, probably only sixteen regularly attending adult males. Furthermore, the birds at this lek had been trapped with cannon nets in the immediately preceding years. The small size or human disturbances perhaps enhanced the instability of this lek. The number of females never exceeded ten nor showed any consistent localization until 27 March, when females congregated in the area used by male D and I saw matings for the first time that season. On 29 and 31 March large packs of females assembled in the same position, but before activity had ended each morning the females gradually drifted 8 m south-west (Maps 4, 5a, b). On both mornings male D accompanied the females as they moved. On 1 April somewhat fewer females appeared but they also drifted south-west in the course of the morning. Ten centimetres of snow covered the ground on 3 April, and only a few females visited the lek. The following two mornings females were again numerous, but they clustered immediately at the site where on previous days they had ended the morning, 8 m south-west of the area in which they had originally congregated. Until 5 April I had observed the lek from a blind placed 25 m from the pack of females. On the afternoon of 5 April I erected a second blind (blind no. 2, Map 3) on a platform 1·2 m high, in hopes of obtaining a better vantage for recording the birds' spatial relationships. The new blind was also 25 m from the site at which females congregated. On the morning of 8 April I began to film activity on the lek from this elevated blind, and on that morning for the first time females began congregating at a site 15 m north-west of male D's territory and farther from both of my blinds (Map 9a, b). Especially when the females returned after an eagle had flushed the grouse at 05.28 hours, all the females went to the new site farther from my blinds. After that date most females tended to congregate in this farther area, although on most mornings some females did come to male D's territory. Thus, the longer move in 1968 appeared correlated with the erection of my elevated blind. My presence perhaps did not influence the shorter and more gradual shift in the position of the mating centre. Possibly mating centres are less well localized in small leks. On this same lek Lumsden (1968) and Hjorth (1970) both observed shifts in the positions where females congregated.

In 1969 on the large Dry Sandy Lek, three mating centres that I could clearly observe remained in the same positions throughout the season. In the mating centre I studied thoroughly that year virtually all matings occurred in an area 5 × 8 m.

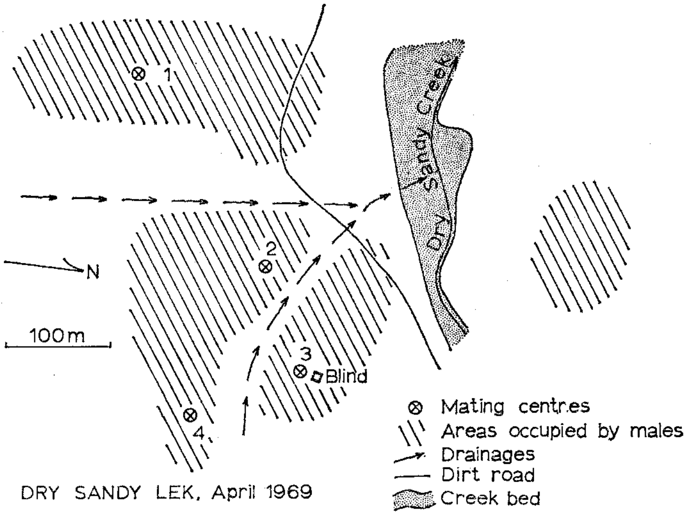


Fig. 9. Four mating centres on the Dry Sandy Lek, 1969. Around each mating centre, 40 to 100 males occupied territories (hatched areas).

Thus shifts in the locations of mating centres have in my experience correlated with unusual disturbances. The balance of the evidence suggests that mating centres, perhaps especially those in the larger leks, normally remain in one place throughout a season and recur in at least approximately the same locations in successive years. Thus the mating centres within a lek apparently show a constancy of location comparable to the traditional locations of the leks themselves.

C. Multiple Mating Centres

On large leks more than one mating centre forms, so that no more than sixty to eighty territorial males surround each mating centre. For instance, the lek I studied in 1967 with 154 males had two well-defined mating centres. When Scott (1942) observed this lek in 1941 he recorded five mating centres among a maximum of 355 males. The lek I studied in 1969 had over 260 males arrayed around four well-defined mating centres (Fig. 9). Possibly, as Lumsden (1968) and Hjorth (1970) have also suggested, sage grouse evolved such large leks by enhancing a tendency to amalgamate several small leks. The males surrounding each mating centre in a large lek are organized much like an isolated smaller lek of sage grouse or other lek-forming species of grouse. The central males are generally more closely spaced and mate most frequently. Grange (1948) has noted that leks of the sharp-tailed grouse *Pedioecetes phasianellus* in Wisconsin occasionally occur in clusters, a tendency that could represent an intermediate stage in the evolution of multiple, but continuous, leks like those of sage grouse.

VII. TERRITORIALITY AND MATING: A STATEMENT OF THE PROBLEM

An examination of some of the features of territoriality in the sage grouse will define the problem of behavioural regulation of their mating system. After presenting evidence that frequent mating by a male depends on the coincidence of his territory with a mating centre, subsequent sections will examine how such a coincidence might arise.

A. Stability of the Territorial Boundary

The boundary zones of most territories remained relatively constant over the 3 to 4 weeks of my observations each season. Some changes did occur, as I shall discuss below, especially when vacancies arose on the lek. In 1968 many changes occurred, largely because three territorial males disappeared from the lek during my observations and because the position of the mating centre drifted 8 m from its original location. In 1969, on the other hand, most of the fully adult males' territorial boundaries persisted in essentially the same locations throughout the period from 8 to 28 April (Maps 11a, b and c). The territorial boundary is treated more thoroughly in Section IX.

B. Distribution of Matings Among Males

The territorial males varied greatly in their success in mating. Those established within or near a mating centre accomplished virtually all the matings, while most males never mated during the entire season. Tables I, II and III

Table I. Copulations Recorded on the Muddy Springs Lek, East Mating Centre, 1967

Date		Individual males				Unident. periph.	Total no. of completed copulations
		A	C	2W	N		
11 April	AM	10*					10
	PM	2					2
12	AM						0
13	AM	1*					1
14	AM	34	(1)				34
15	AM	(1)	1				1
17	AM	12 (6)	7 (3)	3 (1)	2 (5)		24
18	AM	Absent	6 (3)		1(2)		7
19	AM	Absent	2	4 (1)			6
20	AM	Absent	3	7	2	2, 1	15
22	AM	Absent	2 (1)	2 (1)	2		6
24	AM	Absent		2		2	4
25	AM	Absent		2			2
Total no. of completed copulations		59	21	20	7	2, 2, 1	112 (25)
%		52·7	18·7	17·8	6·3	1·8, 1·8, 0·9	

Maximum number of males around this mating centre = 60 ± 5.
Parentheses enclose the number of interrupted copulations.
*Copulations performed at the nothern site (see Section VI).

Table II. Copulations Recorded on the Fords Creek Lek, 1968

Date	Individual males											Total no. of completed copulations
	D	N	UT	TM	F	A	X	ST	Unident. periph.	B	C	
27 March	7											7
28	2											2
29	14											14
31	6			1								7
1 April	7		(1)	(1)					1, 1			9
3									1			1
4	3					1 (1)						4
5	1			2 (2)					1		(1)	4
8		4 (1)		Absent								4
9		3 (1)	2	Absent	2						Absent	7
10	1	4 (3)		Absent	1 (1)						Absent	6
12		4	1	Absent		2		1			Absent	8
14		10		Absent			1			(1)	Absent	11
15			1	Absent							Absent	1
22				Absent							Absent	0
23			1	Absent							Absent	1
24				Absent					1		Absent	1
25				Absent							Absent	0
Total no. of completed copulations	41	25	5	3	3	3	1	1	5	0	0	87 (13)
%	47·2	28·8	5·8	3·5	3·5	3·5		1·2 × 7				

For explanation see Table I. Maximum no. of males on this lek = 30.

present data on all the copulations I observed during the three seasons of study.

A completed copulation satisfied three criteria: (1) the copulation was not interrupted by another male; (2) the copulating male lowered his tail below the female's tail; and (3) the female terminated the copulation by dashing forward with post-copulatory ruffling (Section IV, B). Vigorous post-copulatory ruffling seemed specific to completed copulations. If a male mounted but did not lower his tail before a neighbouring male interrupted the copulation, the female never showed such vigorous ruffling or persistent preening. A completed copulation presumably inseminated the female, although direct evidence for sperm transfer was not obtained. Since each female probably mates only once each season and almost all clutches are fertile (Section VIII, A), a male's success in mating directly reflects his success in fertilizing eggs.

In the first few days of mating one male performed all the copulations at the mating centres studied in 1967 and 1968. Later each season more males participated in mating, although even then most males apparently failed to mate. In 1967 male A dominated the mating first on the northern site and later 10 m away on the south-western site, until he failed to appear on the morning of 18 April (Table I). At the south-western site females congregated in his territory and to some extent in male C's territory. After male A disappeared, females continued to congregate in C's territory and in A's former territory, which was gradually occupied by male N. Females also extended into the territory of male 2W. In 1968 male D dominated the mating until the mating centre moved 15 m north-west after I built my elevated blind (Table II). Before the mating centre moved, the females had congregated principally within D's territory although they extended slightly into TM's. After the mating centre moved, the females congregated in male N's territory, and this male subsequently dominated the mating. In 1969 snow on the prairie

Table III. Copulations Recorded on the Dry Sandy Lek, Mating Centre No. 3, 1969

Date	Individual males								Total no. of completed copulations
	4	7	3	2	9	8	20	12	
6 April									0
8									0
9	3	1	1						5
11	3 (2)	6 (1)	1						10
14	2, 6*	12*			2*				2
15									0
16	3 (1)		1	(1)					4
17	6 (1)	1			1	1			9
18	2 (1)	9	(1)					1 (1)	12
21		9*							0
22									0
23					2*		3*		0
24									0
26									0
27									0
28									0
Total no. of completed copulations	19	17	3	0	1	1	0	1	42 (9)
%	43·8	41·4	7·3		2·4	2·4		2·4	

For explanation see Table I. Maximum number of males around this mating centre = 52.
*Matings with an abnormal female (see text); not included among completed copulations.

hampered the beginning of my studies, and I could not reach the mating centre I eventually studied until 6 April. I recorded many fewer copulations at this mating centre than at mating centres in the previous 2 years. However, I might have missed more copulations this year than in previous years. For one thing, mating probably began at this mating centre about 4 April. On that date I did see a few matings at mating centre no. 3 from a distance of 250 m, which was as close as I could get on that date. In previous years the first few days of mating had included many copulations, and the packs of females reached maximal sizes then. On 6 April 1969 female numbers were relatively low, and then on 8 April the lek was disturbed by two men arriving in a truck. So in this year I probably failed to record the early matings of the season. In addition I devoted more attention to other problems, so I probably overlooked more matings than I did in previous years.

A female with atypical behaviour visited the lek on four mornings in 1969. On each of these four days this one female copulated repeatedly with as many as four males, but she always appeared unable to complete a normal copulation. She did not raise her tail as normal females do after the mounted male begins to lower his tail. After repeatedly attempting but failing to effect cloacal contact with this female, each male simply dismounted. The female never performed post-copulatory ruffling, nor was her pre-copulatory behaviour normal. Although she remained in one spot while a male strutted around her, she did not ordinarily orient obliquely away from the front of the male as normal females do. The males' repeated treadings on 23 April actually drew blood from the abnormal female's back, which stained the white chest of the males attempting to copulate with her. It is because only one such female appeared on any day, and no other female in other years showed similar behaviour, that I have assumed that the same individual came on each of the mornings. I have not included her attempted copulations in the totals of copulations completed by each male in 1969. Scott (1942) and Patterson (1952) each observed one female that copulated repeatedly.

Males successful in mating are those with territories at or adjacent to a mating centre. In each year two or three males, 5 to 10 per cent of the males present around each mating centre I studied, accomplished over 75 per cent of all completed copulations there (Fig. 10). Since the total number of males surrounding each mating centre ranged from thirty to sixty, most of the males never mated at all. Matings by peripheral males tended to occur late in the morning and late in the season when fewer females were present on the lek and they were more dispersed.

Lumsden (1968) and Hjorth (1970) reported somewhat more even distributions of matings among males on the Fords Creek Lek in 1965 and 1966 respectively. Three males in 1965 (10 to 12 per cent of the males present) completed 68 per cent of fifty-two copulations. Twelve males mated at least once, and no male performed more than 29 per cent of the matings.

C. Mating and Territoriality

Mating is contingent upon occupying a territory. A male, even a peripheral male, mates with impunity within his own territory. Occasionally,

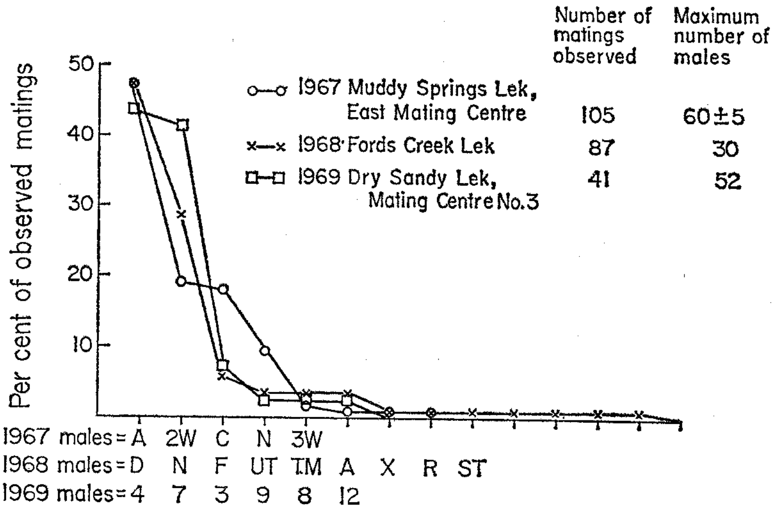


Fig. 10. The distribution of matings among males at three mating centres. Individual males are listed on the abscissa in decreasing order of their successes n mating. The ordinate is the percentage of the total number of completed copulations observed each year.

however, a mating male is interrupted by his neighbour, who dashes in to knock him off the female's back. Such an interruption is usually followed by a facing-past encounter and wing-fighting. None of these interrupted matings was clearly consummated, so in calculating the distribution of matings among males, I have assumed that none of these interrupted matings was successful.

Although a male will intrude beyond the usual zone of facing-past encounters in order to interrupt his neighbour's matings, these incursions are limited to about 1 m. Hence, interrupted matings occur usually near the edges of the males' territories. Map 12 shows the positions of the matings I recorded in 1969 at one mating centre. Most of the matings cluster within the territories of males 7 and 4. Interrupted matings occur only near territorial boundaries, as defined by the zones of frequent facing-past encounters. Also in 1968 interrupted matings mostly occurred near or within the zones of facing-past encounters between neighbouring males (Map 9a).

Interrupted matings represented respectively 18·3, 13·0 and 12·1 per cent of all copulation attempts observed in the 3 years of my study (excluding matings attempted with the abnormal female in 1969). These figures are comparable to those obtained by the Hamerstoms (1955) for prairie chickens *T. cupido* and three to four times greater than figures for black grouse *L. tetrix* (Kruijt & Hogan 1967). Apparently interrupted matings are frequent among prairie chickens because the males often leave their territories when females visit the lek (Hamerstrom & Hamerstrom 1960; Kruijt & Hogan 1967). In contrast, male black grouse remain within their territories even when females are on the lek. In the exclusiveness of their territories, though, male sage grouse seem to resemble black grouse more than prairie chickens (see Section XII). Instead, the high frequency of interrupted copulations in sage grouse might stem from the small size of the males' territories, which had a minimum area of about 25 m^2 in contrast with 75 to 100 m^2 in prairie chickens and black grouse (Section XII). A smaller territory would have a greater fraction of its area close to the boundary. Hence males might attempt copulations more frequently near their boundary, where interruptions are likely. Although one in every six or seven attempted copulations was interrupted, a female's chances for copulation were not limited, since the males seemed always ready to mate again.

Do those males more successful in mating tend to interrupt the matings of their less successful neighbours more than the reverse? The small numbers of interrupted matings I observed cannot provide a conclusive answer to this question (Tables IV, V and VI). In some cases, pairs of neighbouring males interrupted each other's matings almost equally frequently (males C and N, 1967). In other pairs of males one performed more interruptions than the other; however, the male that was interrupted most often sometimes performed more and some-

Table IV. Interrupted Copulations, Muddy Springs Lek, 1967

		Copulating male				Totals
		A	C	N	2W	
Interrupting male	A		1	3	3	4
	C	4		4	3	11
	N	1	6			7
	2W					0
Totals		5	7	7	3	22

Table V. Interrupted Copulations, Fords Creek Lek, 1968

		Copulating male								Totals
		D	TM	UT	B	A	C	N	F	
Interrupting male	D		1							1
	TM	1		1						2
	UT		1							1
	B	1								1
	A						1			1
	C					1				1
	N								5	5
	F							1		1
Totals		2	2	1	0	1	1	1	5	13

Table VI. Interrupted Copulations, Dry Sandy Lek, Mating Centre No. 3, 1969

		Copulating male								Totals
		4	7	3	9	8	12	2	20	
Interrupting male	4		1		1*	1*				3*
	7	1		1						2
	3	3	1							4
	9	2*				1*		1	2*	1, 5*
	8	1			2*				1*	1, 3*
	12				2*				1*	3*
	2									0
	20				3*	1*	1, 2*			1, 6*
Totals		5, 2*	1, 1*	1	8*	3*	1, 2*	1	4*	9, 20*

*Matings attempted with an abnormal female (see Section VII, B). All but two of these interruptions occurred on 23 April.

times fewer matings than his opponent (compare males N and F, 1968, and males A and C, 1967). The males less successful in mating seem to have a greater proportion of their attempted matings interrupted, although these interruptions as usual involve matings near territorial boundaries. If females congregate within one male's territory, then any matings attempted by neighbouring males are likely to occur near the territorial boundary.

In captive flocks of junglefowl, by way of contrast, non-random mating does depend on one male's ability to interrupt others' copulations without himself being interrupted (Lill 1966).

To recapitulate, within his territory a copulating male is largely immune from his neighbours' interruptions. Only matings attempted near or within the zones of facing-past encounters, which define territorial boundaries, risk interruptions by neighbouring males. A male therefore achieves success in mating by occupying a territory that includes a mating centre or part of one, not by directly preventing matings by other males.

VIII. BASES FOR FEMALE SELECTION

How a male's territory comes to coincide with a mating centre depends on behaviour of both the males and females. First, I shall consider the question of how a female chooses where to mate. Since mating centres probably recur from year to year at roughly the same place within a lek (Section VI), females would not need to discriminate any individual differences in the behaviour of the males in order to select a mating partner. Some evidence will indicate that individual differences in the behaviour of males are slight and are not good predictors of a male's success in mating.

A. Behaviour of Females

Before considering how females might select a place to mate, I must describe in more detail the behaviour of females that leads to successful copulation.

Observations on several leks between 16 March and 24 March 1968, suggest that females first appear on the leks in flocks of ten to thirty. Often two or three males in relaxed posture accompany these flocks without performing any displays. These males probably are yearlings, as I shall discuss in a later section (Section IX, J). The loose groups of females wander across the lek without much localization of their movements. The females in these early groups show little behaviour that suggests an inclination to mate. The females usually space themselves 1 to 3 m apart and drift in unorganized fashion across the lek. They assume relaxed postures, preen, and feed. At this stage in the season I never saw females gather in dense packs or perform any precopulatory activities. On several occasions I saw large groups of females fly away from the lek together.

The females exhibited similar behaviour in 1969 when I first arrived at the Dry Sandy Lek. On 31 March and 1 April dispersed groups of females, usually spaced 1 to 3 m apart, wandered irregularly around the lek. Often these groups included males in relaxed posture. The females spent much time preening and showed no precopulatory behaviour. A tendency for dense packing first appeared among the females on 2 April. A maximum of twenty-three females congregated in a dense pack at mating centre no. 1 (see Fig. 9). On 4 April females showed behaviour typical of the mating season. Large, dense packs of females congregated at all mating centres.

As the mating period approaches, the females' behaviour changes in several ways. They form groups away from the mating centres less frequently and leave the lek in large groups less often. These changes in female behaviour are gradual. In 1968 I did see some groups of females that gathered temporarily for periods of 15 to 30 min at sites away from the mating centre, but without the dense packing and signs of precopulatory behaviour that characterize female behaviour at mating centres. Thus as the mating season begins, the gregariousness of the females on a lek decreases, except at mating centres.

On a typical morning during the mating period the distribution of females on a lek progresses through a dispersed phase as females arrive, a congregated phase, and finally another dispersed phase as the females leave. In the hour after sunrise most females are congregated at mating centres; earlier and later more of the females are elsewhere (Fig. 11). In 1969 when I censused females at various times during the morning on a number of days, female numbers on the lek increased rapidly in the $\frac{1}{2}$ hr before and $\frac{1}{2}$ hr after sunrise (Fig. 11). Females usually arrived singly or in small groups; more than five together were unusual. Ordinarily an arriving female would fly straight across the lek, above the strutting males, and utter the distinctive quacking call several times before landing at the periphery of the lek on the far side. On the large Dry Sandy Lek arriving females occasionally alighted within 20 to 30 m of a mating centre, although most landed farther away and nearer the edge of the lek or in areas where males were sparse. Female black grouse, in contrast, tend

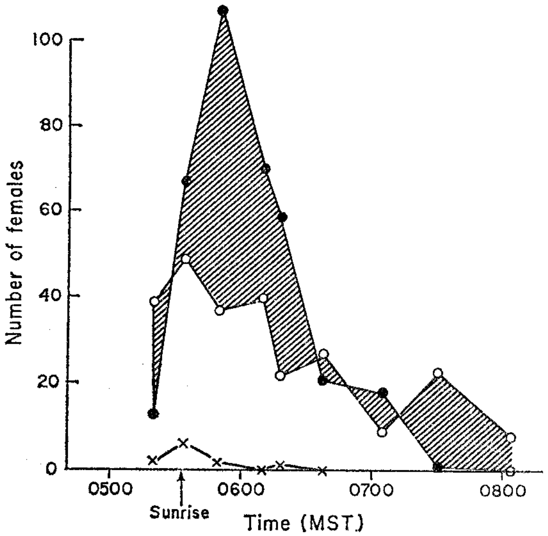


Fig. 11. Numbers of females during the morning of 16 April 1969. Dots, number of females at mating centres; open circles, number of females not at a mating centre; crosses, number of flying females.

to alight in the central territories on a lek (Kruijt & Hogan 1967).

Flying females were most frequent about sunrise (Fig. 11), when the arriving females and their quacking calls stimulated the males to strut persistently. Lumsden (1968) also noticed the quacking call of female sage grouse. He concluded that after arrival females often made short flights from one place in the lek to another and uttered the quacking calls during these flights. My observations, however, suggested that once females had alighted at the periphery of the lek, in most instances they did not take flight again until they left the lek later in the morning. Although the quacking calls occur regularly when females are flying into the lek early in the morning, they are not restricted to this context. Both Lumsden and I heard females give this call occasionally as they took flight late in the morning to fly away from the lek.

After alighting at the edge of the lek, a female usually paused for as long as 1 min and then began to walk. Early in the morning the paths of walking females rarely showed signs of aimlessness. Instead, females ordinarily walked steadily and directly toward the nearest mating centre. In 1968 and 1969 I mapped the paths of a number of females after they had landed at the edge of the lek. Many of these females pursued direct or nearly direct paths toward the nearest mating centre. Occasionally a female would pause briefly before resuming her course or would detour to avoid a male strutting directly in her path. Sometimes a female would increase her pace in order to avoid an approaching male. From my samples of female activity in 1969 I could estimate the fraction of all walking females that were moving more or less toward (± 30°) the nearest mating centre; before and around sunrise the majority of walking females were heading for the nearest mating centre (Fig. 12). When a female came within 15 to 20 m of a pack of females congregated at a mating centre, she rarely stopped or deviated before entering the pack.

On a large lek with several mating centres females did occasionally either walk or fly a short distance from the vicinity of one mating centre to another. In 1969 I observed such behaviour ten times during seven mornings of observation between 9 and 18 April.

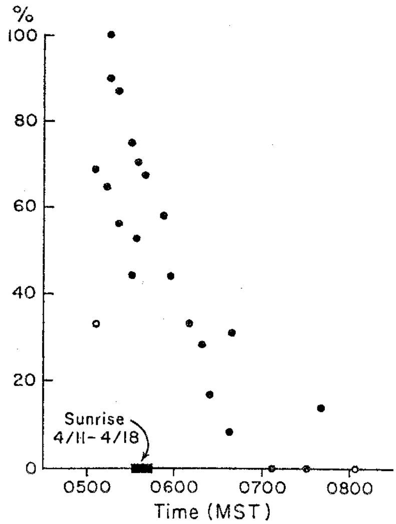


Fig. 12. Females walking toward the nearest mating centre, expressed as percentages of all walking females. 11 to 18 April 1969. Open circles represent samples of fewer than 20 females.

Once in a pack at a mating centre, a female assumed a relaxed posture with her head drawn onto her shoulders. Individual females became extremely difficult to follow within these dense packs. All the females remained in a relaxed posture until ready to copulate. Although the females were usually spaced within a ½ m of each other, aggression between females was limited to low-intensity encounters. Females moved to avoid the path of an approaching bird and moved away from a zone about 1 m in radius around the front of the strutting male. Since the male strutted back and forth within the centre of this pack, females were continuously shuffled in position, usually without much aggression among themselves. Occasionally after the male had approached a female closely or after a female had briefly assumed the precopulatory solicitation posture, she would dash forward a metre or so and chase briefly any female in her path.

On several mornings in 1967 I observed one female that exhibited unusually aggressive behaviour toward the other females. This individual spent most of a morning dashing vigorously after other females, often over distances of 2 to 5 m. If she managed to catch another female, or if another female adopted the solicitation posture near her, she would attempt to mount. A further abnormality was her tendency to erect the feathers on the side of her neck, like a male. I presume that it was the same individual with abnormal behaviour that appeared each of these mornings. She never was seen to copulate. Other observers have noted females that showed similar elements of male behaviour (Scott 1942; Patterson 1952; Lumsden 1968).

Females normally adopted the solicitation posture near the termination of the male's strut. The male waited 7 to 10 s after his previous strut before mounting. Sometimes the female would relax before he mounted and then solicit again following his next strut. Usually if a female continued to solicit in this way, she progressively increased the duration and intensity of her solicitation posture. Eventually a female might hold her solicitation posture continuously between successive struts of the male. Ordinarily a female did not solicit except when she was within ½ m of the front of the male, but intensely and persistently soliciting females sometimes assumed their posture more than 1 m from the male. Usually the male mounted any female that would hold a solicitation posture while he stepped toward her. Occasionally, though, especially later in a morning a female would solicit repeatedly and intensely after five or more struts before the male mounted. Once a male mounted, copulation was usually completed in 3 to 5 s, unless a neighbouring male interrupted the copulation. Thus, although copulation itself was brief, continued interaction of a male and a female appeared necessary to stimulate both sexes to copulate.

Most females probably mate only once a season. By observing sixteen marked females, Lumsden (1968) noticed that females visited a lek on several mornings before they were seen to mate, while none of the seven females observed mating was ever seen again. Pyrah (1964) records a captive hen that laid six fertile eggs after she was removed from any contact with males. Her last fertile egg was laid over 17 days after she could possibly have copulated. Thus one copulation apparently fertilizes a female's entire clutch, which averages six to eight eggs. On the other hand, the number of copulations that occur at a mating centre probably exceeds the maximum number of males surrounding the mating centre. At the mating centres studied in 1967, 1968 and 1969, I recorded 1·8, 2·9 and 0·8 times as many copulations as males. Since I did not observe the leks continuously, I must have missed many matings, so the ratios of copulations/total males must actually exceed these figures. If some females copulate more than once in a season, the number of copulations might well exceed the maximum number of males. However, ratios greater than one might also reflect an unequal sex ratio at that season, or the absence of some males from the leks. Particularly some of the yearling males might not attend the leks regularly, and thus at any one time a proportion of the males might not appear on the leks. Only further studies of individually marked females will clarify these problems. Available evidence suggests that each female visits a lek on several mornings in a season, mates once or perhaps occasionally twice, and then lays her entire clutch of eggs after leaving the lek.

Essentially, all yearling females breed, as Dalke et al. (1963) have determined by examining the ovaries of females shot during the autumn hunting season, when yearlings still carry their outermost juvenile primaries. Furthermore, over 94 per cent of all eggs are fertile (Patterson 1952).

Following a completed copulation, a female usually moved to the edge of the pack of females or somewhat beyond. After shaking herself violently a number of times (post-copulatory ruffling) she began to preen thoroughly, especially her breast and scapular region. In 1969 a number of females were followed after copulation. Eventually these females would reduce their preening activity and begin to walk slowly and irregularly toward the edge of the lek. They usually avoided close approaches by peripheral males. Finally they were lost in the sagebrush 25 to 50 m from the mating centre. Some flew directly away from the lek.

As the morning progressed females began to leave. At first they drifted irregularly away from the pack and spent considerable time preening or feeding on sagebrush. Beginning an hour or so after sunrise single females or pairs flew away from the lek. Occasionally a female would fly directly from the pack at a mating centre. Usually, however, females first wandered away from the pack into the periphery of the lek and then flew off. Later in the season the packs of females that congregated each morning at the mating centre became smaller. When the pack did not exceed about ten females, females appeared to spend more time in the periphery of the lek. During this period, following the initial peak of mating activity, some of the peripheral males performed occasional copulations.

To recapitulate, females appeared early in the season in loose groups that wandered apparently aimlessly around the lek. When mating began the tendency of females to move in flocks across the lek decreased. Females never flew directly to a mating centre on arrival in the morning. Instead they usually flew over the lek, landed in the periphery, and then walked to the mating centre. The relatively direct paths of females walking toward a mating centre early in the morning suggests that many individual females knew at least approximately where the mating centre was located.

On the basis of this analysis of their behaviour, it seems reasonable that females might use any of six sorts of cues to locate a mating centre: (a) individual differences among the males that correlate with their success in mating; (b) overall patterns in the distribution or activity of males within a lek; (c) topographical or vegetational characteristics of mating centres; (d) the presence of a conspicuous pack of females at a mating centre; (e) guidance from other females that had visited the mating centre previously; and (f) memory of the topography of the lek after her first few visits. The following sections will consider these possibilities in turn.

B. Individual Differences Among Males

Evidence presented in Section VI suggests that mating centres recur from year to year at roughly or precisely the same sites within a lek. This stability in the locations of mating centres could conceivably depend on the presence from year to year of the same individual males on the lek. However, yearly mortality among fully adult males, two or more years old, probably approximates 25 to 50 per cent (Section X), so the turn-over of individual males on any lek from year to year must be considerable.

I was unable to find differences among individual males' struts that correlate with differences in mating success. The strut display is remarkably stereotyped in its internal organization, as I have determined from an examination of filmed sequences of different males' displays. The means for the different males are extremely similar, and the small differences do not correlate with mating success. Data supporting this point will be published elsewhere.

Nor do the successful males appear to respond to the presence of females more vigorously than do other adult males that rarely or never mate. The frequency of strutting and facing-past encounters often differed considerably at any one time between central and peripheral males. However, these differences seem best explained by the proximities of the different males to females, rather than by intrinsic differences in the behaviour of individual males.

Rates of strutting by successful and unsuccessful males were compared when females were either near them or farther away. Data were taken from twenty-eight 6 min sequences of time-lapse film from 1968 (Section V, H). On the days used for sampling male D performed most of the matings. Eight individual males were included in at least eight of the twenty-eight samples. All of these males were at least 2 years old; the behaviour of yearling males will be discussed in a subsequent section (Section IX, M). In Fig. 13 the black histogram for each male indicates the number of 6-min periods with different rates of strutting when at least one female was within the male's territory (situation T); the stippled histogram for each male presents rates of strutting when females were within 10 m in a neighbouring territory (situation N); the open histogram for each male presents rates of strutting when no females were within 10 m of the male (situation O). Males strutted at rates of twenty-one to forty-three struts per 6 min when females were present within their territories, and all males strutted much less frequently when no females were nearby. The wide dispersion of the strutting rates in situation N probably indicates that this category was heterogeneous. Either males responded to females in neighbouring territories with considerable variability, or I failed to isolate effectively the cues to which the males responded. By comparing the black histograms (situation T) for the males sampled, I could establish only one statistically significant difference in their responses to females in their territories: Male D, who did most of the mating, tended to strut less frequently than his

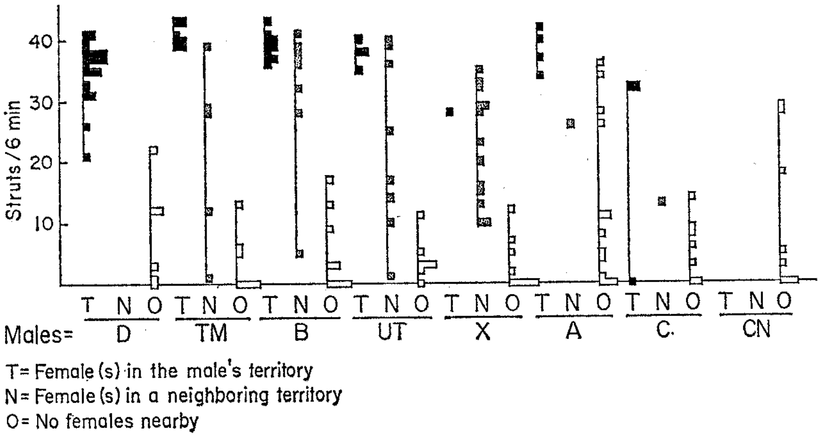


Fig. 13. Eight individual males compared for differences in their rates of strutting in three situations: female(s) within the male's territory (black histograms, T); female(s) within 10 metres in a neighbouring territory (stippled histograms, N); and no females nearby (open histograms, 0). The ordinate is struts per 6-min period. In the histograms each small square represents data from one 6-min period.

neighbour, male B, who never mated successfully (Wilcoxon matched-pairs ranked-sign test, $T = 2{\cdot}5$, $N = 10$, $P<0{\cdot}01$; Siegel 1956).

Male D's lower rates of strutting are not explained by interruptions for matings or other activities. Instead, male D in comparison with his neighbour, male TM, often strutted less frequently per minute in strutting posture (Table VII). Fatigue may explain male D's slower rate of strutting. Late in the morning his matings and his rates of strutting near females were noticeably slower. In 1967 the most successful breeder also showed signs of fatigue on mornings when females were numerous. Late in the morning his matings often became noticeably slower, and he was slower to resume strutting after facing-past encounters. Scott (1942) noticed similar signs of fatigue late in the morning among males that mated frequently.

The sample in which male D strutted least frequently with females in his territory, twenty-one struts per 6 min, came nearly 2 hr after sunrise, near the end of the morning's activity. In general, though, rates of strutting show little correlation with the time of morning, provided the males' proximities to females are taken into account (Fig. 14). Males with females in their territories strut at high rates regardless of the time of morning.

Only far more data of a similar sort would allow completely satisfactory comparisons of a number of males under conditions of comparable proximity to females. The present data, though, do suggest that most of the variability in rates of strutting is explained by the males' proximities to females, rather than by their positions on the lek or the time of morning. Figure 15, based on the same data, emphasizes that males strut at high rates more often when females are in their territories. Although males established at a mating centre must strut many more times in a morning than do more peripheral males, their greater persistence in displaying stems from their persistent association with the females (Section

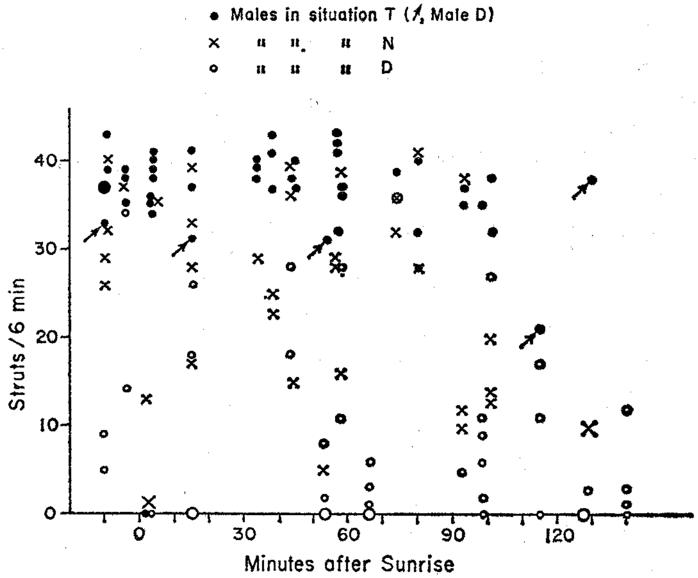


Fig. 14. Rates of strutting in relation to time of morning and proximity to females. Black dots: males with females in their territories. Crosses: males with females within 10 metres in a neighbouring territory. Open circles: males with no females nearby. Data from 27 March to 1 April 1968. Larger symbols indicate more than one male with that value. Arrows indicate extreme values for Male D in situation T.

Table VII. Numbers of Struts per Six Minutes in Strutting Posture; Comparison of Five Males When Females Were in Their Territories (Situation T)

	Individual males				
	D	TM	B	A	UT
Mean	37·4	42·8	39·8	38·6	40·2
No. of samples	22	7	10	4	4
SD	4·76	1·65	2·09	3·99	0·35
SE	1·02	0·62	0·66	1·99	0·18
Seconds/strut (= 360/$\bar{X}$)	9·62	8·41	9·05	9·33	8·95

Differences between males (Mann–Whitney U tests): D–TM, $U = 7$, P (two-tailed) $<0·001$; D–B, $U = 74·5$, P(two-tailed) $>0·1$; all other differences also insignificant.

IX, E), rather than the converse. Territorial males appear to show no obvious differences in the form or rate of their strutting that would explain the differences in their mating success.

Kruijt & Hogan (1967) have suggested that female black grouse (*L. tetrix*) might approach males that fight frequently. In sage grouse the behaviour of central and peripheral males during facing-past encounters does differ. Here, too, these differences are probably a consequence rather than a cause of female proximity. Again I have relied on the twenty-eight 6-min samples of male activity in 1968 to obtain the durations of facing-past encounters when the opponents were at various distances from females (Table VIII).

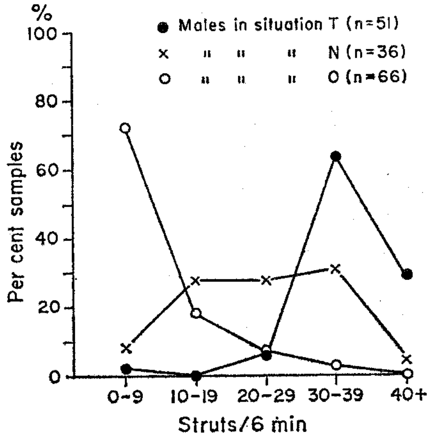


Fig. 15. Rates of strutting at different distances from females.

Table VIII. Relationship Between the Durations of Males' Facing-Past Encounters and Proximity to Females

Proximities of opponents to females	Durations of facing-past encounters							No. of encounters with wing-fights
	1–35 (s)	36–60 (s)	1·0–1·9 (min)	2·0–3·9 (min)	4·0–5·9 (min)	6·0+ (min)	Total no. of encounters	
T–T*	14^{ab}†	4					14	2
T–N	5	4					9	3
N–N	3^{bc}	2	2	3	1		11	0
N–O	3	2	3	2	1		11	0
O–O	6^{ac}	4	5	6	2	9	32	5
T–O		1		1		1	3	0

Figures in the table are numbers of encounters. Data from twenty-eight 6-min samples, 27 March to 3 April 1968.
*T–T signifies that both opponents had females within their territories (situation T). A male in situation N has a female within 10 m in a neighbouring territory. A male in situation O has no female nearby.
†Comparisons: a, χ^2 (Yates correction) $= 22·96$, $P<0·001$; b, χ^2 (Yates correction) $= 11·82$, $P<0·001$; c, χ^2 (Yates correction) $= 0·029$, $P>0·80$.

When both opponents had females within their own territories (situation T–T) encounters invariably terminated within 35 s. In fact, most of these encounters probably terminated within 10 s. In contrast, when neither opponent was within 10 m of a female (situation O–O), the durations of their facing-past encounters showed great variability, but 33 per cent lasted 4 min or longer.

Both opponents apparently influence the durations of their facing-past encounters in accordance with their proximities to females. If only one opponent has females within his territory (situations T–N and T–O), encounters are often longer than if both males have females within their territories (situation T–T) (Table VIII). Therefore, the durations of a male's facing-past encounters depend both on his own and on his opponent's distance from females.

It is uncertain whether these trends correlate with individual differences among the males as well as with the proximity of the males to females. The data are too few to allow many comparisons of the same pairs of males at different distances from females. When individual males are considered separately, the data reveal no appreciable individual differences in the durations of facing-past encounters independent of differences in proximity to females (Table IX).

Frequencies rather than the durations of facing-past encounters might differ among individual males. Comparisons among the males

Table IX. Durations and Frequencies of Facing-past Encounters by Individual Males at Different Distances from Females

Proximity to females	Male	Durations of encounters						No. of encounters			No. of samples
		1–35 (s)	36–60 (s)	1–1·9 (min)	2–3·9 (min)	4–5·9 (min)	6·0+ (min)	Total	Initiated	Terminated	
T	D	15	1	1				17	17	17	22
	TM	8						8	8	8	7
	B	4						4	4	4	10
	A	1						1	1	1	4
	UT	2	2					4	4	4	4
	X			1				1	1	1	1
	C	1					1	2	1	1	3
	CN							0			0
	Subtotals								36	36	51
N	D							0			0
	TM	3	4	3	3			13	11	10	5
	B	3	1			1		5	5	4	8
	A							0			1
	UT	3	2	2	5			12	10	11	8
	X	2	3	2	2			9	8	7	13
	C							0			1
	CN	1						1			0
	Subtotals								34	32	36
O	D		1				1	2	2	0	6
	TM	2	1	1	3		1	8	6	5	7
	B	2	1	1	4		4	12	7	7	9
	A	5	1		3	2	4	15	9	9	13
	UT		2	4	2		1	9	6	6	7
	X	1			3		1	5	1	4	9
	C		1	2	1		2	6	2	4	6
	CN	1	2	2	1		3	9	4	6	8
	Subtotals								37	41	65
	Totals								107	109	152

are complicated by two considerations: (a) each encounter involves the interaction of two individuals, so a male's behaviour is influenced both by his own tendencies and by his neighbour's; and (b) different males have different numbers of neighbours. In order to minimize the effects of these complications, I determined the frequencies of facing-past encounters for pairs of males, rather than for individuals, when each male's proximity to females was known (Table X). Although the rate of terminating encounters often differed slightly from the rate of initiations, these differences must be artifacts of my small samples, since in the long run the rate of terminations should equal the rate of initiations of facing-past encounters. For pairs of males other than D–TM and D–B, encounters were most frequent in situations T–T (0·27 initiations per 6 min) and O–O (0·24 initiations per 6 min) and least frequent in situation T–N (0·04 initiations per 6 min). Between male D and his neighbours B and T, encounters are most frequent in situation T–T (0·47 initiations per 6 min), of intermediate frequency in situation T–N (0·31 initiations per 6 min), and least frequent in situation O–O (0·09 initiations per 6 min). Thus, the most successful breeder (male D) encountered his neighbours, B and TM, least frequently when neither had females nearby (situation O–O), while other pairs of males encountered each other least frequently in situation T–N, when one of them had females in his territory. However, the available data are far too few for any definite conclusions. Encounters were always most frequent when two neighbours both had females within their territories. Since in these cases the females usually occurred near the two neighbours' common boundary, a high frequency of facing-past encounters would be expected.

Do those males successful in mating engage in wing-fighting more frequently than others? Table XI presents the incidence of wing-fighting in all facing-past encounters recorded for seven pairs of males filmed on mornings in 1968 when females were numerous (27 March to 4 April, except 3 April). Encounters that occurred earlier than 1 hr after sunrise are separated from ones that occurred later, when females were less numerous on the lek, although not absent. The pairs of males are grouped into three categories depending on their distances from the mating centre in the territory of male D. In all three categories wing-fighting occurred in approximately one-fifth (0·18 to 0·21) of the earlier

Table X. Frequencies with which Neighbouring Pairs of Males Initiated Facing-Past Encounters in Situations T–T, T–N, and O–O

		Total no. of encounters initiated (and terminated)	No. of 6-min samples	Initiations per 6 min
Situation T–T	Pairs D–TM and D–B	8 (8)	17	0·47
	Other pairs	4 (4)	15	0·27
	Totals	12 (12)	32	0·37
Situation T–N	Pairs D–TM and D–B	4 (5)	13	0·31
	Other pairs	0 (0)	26	0
	Totals	4 (5)	39	0·10
Situation O–O	Pairs D–TM and D–B	1 (0)	11	0·09
	Other pairs	9 (12)	38	0·24
	Totals	10 (12)	49	0·20

Table XI. Proportion of Facing-Past Encounters that Included Wing-Fighting, 27 March to 1 April 1968

Opponents	Earlier than 1 hr after sunrise: Total no. of encounters	Earlier than 1 hr after sunrise: Proportion with wing-fighting	Later than 1 hr after sunrise: Total no. of encounters	Later than 1 hr after sunrise: Proportion with wing-fighting
D–TM	34	0·21	13	0·15
D–B	15	0·20	3	0
D–X	5	0·20	3	0·33
Subtotals	54	0·204	19	0·158
TM–UT	11	0·27	10	0·10
B–A	6	0	5	0·20
Subtotals	17	0·176	15	0·133
A–C	7	0·57	9	0·11
C–CN	17	0·06	6	0
Subtotals	24	0·209	15	0·071
Grand totals	95	0·200	49	0·140

Difference between earlier and later in the grand totals is just significant at 0·05 level: $\chi^2=3{\cdot}95$, $0{\cdot}02<P<0{\cdot}05$. No other comparisons show significant differences.

facing-past encounters. Later in the morning the frequency of wing-fighting declined in all three groups, and the difference is significant in a χ^2 test. Male D's higher incidence of wing-fighting late in the morning might depend on the regular presence of a few females in his territory until late in the morning. These observations again suggest that differences in the males' behaviour relate primarily to differences in their proximities to females.

In conclusion, these studies of territorial male sage grouse at least 2 years old have revealed no clear differences in their behaviour patterns or responsiveness to females that might explain the large differences in their mating success. The individual differences I did detect among males do not correlate with their differences in mating success. If the females use individual differences in the behaviour of males to select a place to mate, they must depend on subtle distinctions, for the obvious differences between males successful in mating and those unsuccessful depend on the presence of females at the mating centre. For instance, the males' behaviour during facing-past encounters and their frequencies of strutting depend primarily on their proximities to females and only secondarily correlate with the males' successes in mating.

Kruijt & Hogan (1967) have suggested that males successful in mating might employ better tactics in their interactions with females. I could not detect any obvious temporal or spatial patterns in the behaviour of successful males that would impart some advantage in attracting or keeping females within their territories. Definite conclusions about possible male tactics, however, must await further quantitative studies of their behaviour.

This section has only considered males at least 2 years old. Yearling males differ from older males in several ways, as I shall describe in Section IX, M.

C. Density of Males' Territories

Females might use patterns in the aggregation of males to determine the approximate location of a mating centre, since the males' territories are usually smaller near a mating centre (Section IX, A).

As they fly across the lek arriving females would have the opportunity to assess the density of males in various parts of the lek. During this period of the morning almost all the males on the lek strut persistently; apparently the females' arrival and their quacking calls stimulate the males to strut. So a female could probably recognize areas where males are more densely spaced, as they are around the mating centres. The sizes of male territories, however, would not completely specify the positions of the very localized mating centres. Although territories are generally smaller in the vicinity of a mating centre, usually several territories elsewhere are as small as those in which the mating centre is located (Maps 3 and 11a). Furthermore, since males often confine most of their activities to a small portion of their territories, especially when females have congregated at the mating centre, it might prove difficult for a female to assess the size of any particular male's territory. The overall density of males would thus specify the general area of the mating centre but not its exact location.

D. Surface Features of the Lek

Surface features of a lek probably do not determine the locations of mating centres. In all 3 years many other areas seemed identical to the mating centres in sparseness of sagebrush and presence of sod-forming grass. However, the mating centre I observed in 1967 did acquire a distinctive surface feature, since the large packs of females tore the short grass down to its roots. The location of the mating centre became easily apparent even in the absence of the grouse. The packs of females in 1968 were never so large, and I noticed no signs of trampling on the lek. In 1969 little grass grew on the lek. The mating centre I observed occupied part of an area in which sagebrush was unusually sparse and the ground was almost bare. A number of other such areas had no mating centres, although males occupied territories there as well as in areas of thicker sage. At this lek I noticed no permanent modification of the surface by the packs of females.

E. Other Females

Might females use cues from other females when they locate a mating centre? Females usually arrived at a lek singly or in small groups and then subsequently aggregated at a mating centre after walking from the periphery (Section VIII, A). I attempted to determine whether arriving females tended to pause near other females. Such behaviour would provide one possible mechanism for the aggregation of females at a mating centre. Data from my samples of female activity in 1969 suggest that females pausing away from a mating centre are indeed associated with other females significantly more often than are walking females ($N = 500$, $\chi^2 = 14{\cdot}11$, 1 *df*, $P < 0{\cdot}001$). In comparison with females which paused farther than 3 m from a male, females which paused near a male are more often near other females ($N = 267$, $\chi^2 = 5{\cdot}37$, 1 *df*, $P < 0{\cdot}05$). Yet females pausing farther than 3 m from males associate with other females no more often than do walking females ($N = 360$, $\chi^2 = 2{\cdot}88$, 1 *df*, $P < 0{\cdot}05$) Therefore, females pausing away from the mating centre apparently are attracted either to a strutting male or to the combination of a paused female and a strutting male.

A cluster of taxidermic models of females was used on 17 April 1969 in an attempt to decoy females approaching a mating centre. I placed an artificial pack of five taxidermic mounts of females 15 m from the mating centre. The decoys failed to attract any live females, although a number walked directly past on their way to the mating centre. The negative result is inconclusive since most of the females this late in the season had probably already visited the mating centre at least once on a previous morning. So no direct evidence can confirm that individual females interact in locating the mating centre. However, this possibility seems so likely that further experiments would be worthwhile.

Possibly a female first identifies the position of a mating centre by seeing the conspicuous pack of females there. Further guidance might come from the more intense activity of males near a mating centre, once most of the females had congregated there (Section VIII, B). In either case, some females must recognize the position of the mating centre independently of stimuli contingent upon other females. Many females visit a lek on several mornings before copulating. Those arriving later in the season might use cues from earlier arrivals to locate the mating centres, provided that females on their first visits arrive later in the morning than do females that have been there several times before. After visiting a mating centre several times in one season, females might remember at least the approximate location from day to day and possibly from year to year.

If yearling females mate later than older females in the course of each season, they might learn the position of a mating centre by tradition. When trapping females on leks in Montana, Robert Eng (personal communication) found indications that yearling females do tend to appear on the leks later in the season than older females. Dalke et al. (1963, p. 836) also suggest that yearling females breed later than older females. Differences in the behaviour of yearling and older females invite further study.

F. Summary

Much of the variability in the behaviour of different males on a lek depends on their different proximities to females rather than on inherent differences among the males and thus represents a consequence rather than a cause of the females' movements. A female probably uses a number of different cues to find the mating centre and possibly different ones on her first visit as a yearling than on later visits. Since the mating centres apparently recur from year to year at the same sites within leks, females choosing a place to mate would not have to rely on individual differences among the males. Present evidence suggests that the density of male territories and the surface features of a lek do not completely specify the positions of the narrowly localized mating centres. However, the density of male territories would provide some orientation for an arriving female. Further cues might come from other females that remember the position of a mating centre from previous visits. Table XII summarizes the cues that a female might use in locating a mating centre.

Table XII. Sources of Information Available to Arriving Females about the Location of a Mating Centre: A Tentative Classification

Type of stimulus	Specificity for the location of the mating centre	Availability to arriving females
Individual differences in the behaviour or morphology of males	Not specific	Whenever males present
Density of male territories	Specifies general area only	Whenever males present
Topographic or vegetational features of mating centres	Ambiguous	Always available
Presence of a pack of females at the mating centre	Specifies exact location	Not available to females arriving earliest in morning
Memory of location	?	Not available to females on their first visit
Behaviour of experienced females	?	Whenever in the company of an experienced female

IX. INTERACTIONS OF TERRITORIAL MALES

To turn now to the males: how does a male acquire a territory at a mating centre? This inquiry will lead to the recognition of several sorts of polarity in territorial males' interactions. These polarities all depend on the attractiveness of the mating centre for the males.

A. Territory Size and Exclusiveness

Using Maps 1, 3, 11a, I estimated the sizes of territories on each lek by averaging two measurements with a planimeter of each territory (Tables XIII, XIV and XV). Boundaries were well documented where two neighbours frequently met in facing-past encounters, or where an individual's movements coincide with some surface feature of the lek (further details in Section IX, B). Other boundaries, especially those of peripheral territories, were either poorly demarcated by the birds' movements and facing-past encounters, or poorly recorded in my notes and films. In Tables XIII to XV, the designated territories had at least one poorly known boundary, so I could only crudely estimate their areas.

Territories near a mating centre tend to be smaller than more peripheral ones. The general

Table XIII. Sizes of Territories on the Muddy Springs Lek, 1967

Resident male	Area (m^2)	Distance from mating centre*	Accuracy**
A	15·4; absent†	0	Good
N	19·6; 24·3	0	Good
C	22·0; 13·3	0	Good
2W	29·1; 39·6	1	Good
SE	⩾29; 44	1	Poor
E	No data; 28	2	Poor

*Number of territories intervening between the measured territory and the mating centre. 0 indicates the measured territory included part of the mating centre.

**Accuracy was poor when at least one boundary was poorly determined (see text).

†Left figure: 17 April. Right figure: 19 to 25 April.

Table XIV. Sizes of Territories on the Fords Creek Lek, 3 to 5 April 1968

Resident male	Area (m^2)	Distance from mating centre	Accuracy
D	33·6	0	Good
TM	36·2	1	Good
B	48·8	1	Good
C	16·7	2	Good
X	46	1	Poor
UT	85	2	Poor
A	22	2	Poor
N	67	2	Poor
ST	⩾68	2	Poor
F	⩾62	3	Poor

See Table XIII for explanation.

Table XV. Sizes of Territories on the Dry Sandy Lek, 8 to 28 April 1969

Resident male	Area (m^2)	Distance from mating centre	Accuracy
4*	17·0	0	Good
7	26·3	0	Good
3	24·0	1	Good
6	13·8	1	Good
9	15·8	1	Good
8	13·5	1	Good
2	21·2	2	Good
20	12·4	2	Good
12	22·7	2	Good
27	49	1	Poor
19	51	1	Poor
14	⩾57	2	Poor
13	⩾63	2	Poor
16	⩾54	3	Poor
21	45	3	Poor
22	⩾40	3	Poor

See Table XIII for explanation.
*After 18 April.

decrease in territory size away from the mating centre was especially clear on the large leks studied in 1967 and 1969. Those near a mating centre usually did not exceed 8 m in diameter, while those towards the periphery of the lek often reached 12 m in diameter. A peripheral territory resembled the more central ones in that the area enclosed by zones of facing-past encounters was used almost exclusively by one male. Although with larger territories the locations of facing-past encounters between neighbours may be less stable, any increase in dispersion of facing-past encounters was not large in relation to the increased diameters of the territories.

Another trend is evident in Tables XIII to XV: the territories near the mating centre on the Fords Creek Lek in 1968 were larger than the central territories in 1967 and 1969. This difference might reflect either the smaller number of males on the Fords Creek Lek or the instability in the location of the mating centre (see Section VI), which in turn might have resulted from the fewer males or from disturbance of this lek by myself or earlier workers (see Sections I and VI). It is an intriguing possibility that smaller leks might in general show less stable organization than larger ones.

Each male tended to concentrate his strutting on that side of his territory nearest a pack of females. Thus when a group of females was present at a mating centre, the males on neighbouring territories spend most of their time strutting in the portions of their territories nearest the mating centre, usually in or close to the zone of facing-past encounters. Male 8 in 1969 provided a good example of how a male's use of his territory depended on the positions of females. Map 13 compares the positions in which male 8 strutted in a typical period with females present at the mating centre in the territories of males 7 and 4, and the positions in which he strutted when a small group of females lingered temporarily in the territories of males 9 and 20 one morning. In the latter instance male 8 and male 13 actually trespassed as much as 2 m beyond their usual zones of facing-past encounters.

Strutting males only occasionally transgressed their boundaries and almost never further than male 8 did on this occasion. Males at least 2 years old avoided deep intrusions into each others' territories. Exceptions occurred occasionally when males were walking to their positions on arrival at the lek (Section IX, L) or when a series of males abandoned their positions in order to follow a flock of females leaving the lek early in the season (Section IX, G). In the former case, when males had to cross an occupied territory to reach their own, they always adopted a relaxed or sleeked posture, detoured around the resident males, and ran or flew, if necessary, to avoid them.

When a strutting male encroached beyond his usual zone of facing-past encounters, as did males 8 and 13 in the example discussed above, they usually retreated immediately to the zone of facing-past encounters when the resident male initiated an encounter. Since these encroachments occurred most often when a male had females in his territory, he would only occasionally interrupt his strutting around the females to challenge his encroaching neighbours. In the case discussed above, male 8 actually encountered male 9 slightly beyond their usual zone of facing-past encounters, although not so far beyond as male 8 managed to strut in the intervals between his encounters with male 9. A similar case occurred on 14 April 1968 when male N had many females within his territory (Section VI). On this morning his neighbours X and UT transgressed their usual boundaries and encountered male N 5 m beyond their usual zones of facing-past encounters (Maps 9a, b). Usually, however, a strutting male, after encroaching slightly into a neighbouring territory, retreated to his usual zone of facing-past encounters when challenged.

An inhibition against intruding into neighbouring territories became especially evident in two situations. When male A disappeared in 1967 and left a vacancy that included part of a mating centre, the vacancy was only gradually reoccupied over a period of several days (Section IX, H). Secondly, males did not intrude deeply into neighbours' territories to interrupt copulations (Section VII, C).

B. Nature of the Territorial Boundary

Zones of facing-past encounters were usually unrelated to the occurrence of clumps of sagebrush or other distinctive features on the ground. In a few cases in which these zones were adjacent to isolated clumps of sage, the zones were always stable. In 1968 a large clump of sage lay just east of the area habitually used by A and C for their facing-past encounters (Maps 5b and 8b). In 1969 males 3 and 6 met each other just south of an isolated clump of sage (Map 11c). In both these cases, although individual encounters often did not occur in precisely the same spots, nevertheless the zones of facing-past encounters remained stable over periods of 3 to 4 weeks. However, other males' boundaries that did not coincide with physical or vegetative features of the ground remained just as stable. Presumably the males remember the locations of sagebrush clumps and other features of the surface in order to occupy the same positions and encounter their neighbours in the same zones over several weeks.

The radial and circumferential extent of the zones of facing-past encounters between different pairs of males showed considerable variation. The most peculiar territory of any male studied closely was that of male 8 in 1969 (Maps 11a, b, c). The area in which he strutted was long and narrow, 2·5 × 10 m. I have already indicated that he chose positions for strutting, usually near one end or the other, depending on where he could get closest to females. His encounters with male 13 were strung along the entire length of his territory and showed such variability in their locations that at one time or another encounters with male 13 occurred throughout the width of male 8's territory (Map 11c). Males 9 and 2 in 1969 also encountered each other along a boundary line 5 m in length (Map 11c), yet their zone of facing-past encounters had less radial dispersion. In 1968 male B, in a similar way, tended to encounter his neighbours, males D and TM, at positions along a boundary line. In contrast, his encounters with male A usually occurred near one site (Maps 5b and 8b). Similarly, in 1969 male 6 met his neighbours, males 3 and 9, in comparatively circumscribed areas 2 to 3 m in diameter (Map 11c). Thus, some neighbouring pairs encountered each other near specific spots, while other pairs met each other at many sites along a boundary line. Every sort of gradation occurred between the two extremes.

The radial variability in the positions of facing-past encounters between neighbouring males did not seem to relate closely either to the frequency with which the males encountered each other or to the circumferential dispersion of the encounters. All possible combinations occurred. Considerable radial dispersion in the positions of encounters appeared both when encounters were dispersed circumferentially along a boundary line (males 8 and 13, 1969, Map 11c) or when they were confined to the vicinity of one spot (males A and C, 1968, Map 8b). Lower variability also occurred in both situations (males 8 and 4, 1969, compared with males 3 and 6, 1969, Map 11c). In 1969 male 9 met male 2 frequently and male 4 infrequently, but his encounters with both seemed to have little radial dispersion (Map 11c). In 1968 male C met both his neighbours, males A and CN, frequently but with considerable radial dispersion (Map 8b). So the circumferential extent of the zone of facing-past encounters between neighbouring males lacked consistent relationship with the radial dispersion of the zone or the frequency of their encounters.

Pairs of males showed little evidence of selecting conventional sites at which to encounter each other. The shapes of the zones of facing-past encounters between pairs of neighbouring males depended largely on the males' activity patterns within their territories. If two males habitually strutted at particular sites within their territories, most of their encounters occurred near the intersection of the boundary zone with a line between the two strutting males. In a few cases surface features of the lek influenced the positions of facing-past encounters. For instance, in 1968 male A met male C, and later in the season male CN, at positions between a large clump of sage to the east and a depression of the ground to the west (Maps 8a, b and 9a, b).

C. Initiation of Facing-Past Encounters

The initiations of facing-past encounters provide evidence of non-reciprocal interactions between territorial males, a polarity that results from the attractiveness of the mating centre for territorial males.

When females are present at the mating centre, each male tends to strut along the side of his territory nearest the mating centre (Section IX, A). Periodically his more central neighbour initiates an encounter with him, since a male strutting near or within his territorial boundary, as defined by the zone of facing-past encounters, presents a prime stimulus prompting his nearest neighbour to initiate a facing-past encounter. Consequently, the more peripheral of two neighbours is more prone to encroach into or beyond their usual boundary, and the more central one tends to initiate more of their facing-past encounters.

To quantify this trend I have classified facing-past encounters between different pairs of males according to how they were initiated. I recognized three kinds of initiations: by one or the other male, and mutually. In a mutual initiation the two opponents started toward each other so nearly simultaneously that I could not distinguish which one actually began. In most situations, however, I could easily decide which male initiated the encounter. Uusally one male dashed toward his opponent, who was strutting or, occasionally later in the morning, sitting in semi-relaxed posture near the zone of facing-past encounters. In mutually initiated encounters both males usually dashed to meet each other in the zone of facing-past encounters. Especially later in the morning males often walked, rather than ran, to encounter their neighbours. Occasionally a male would walk to his boundary

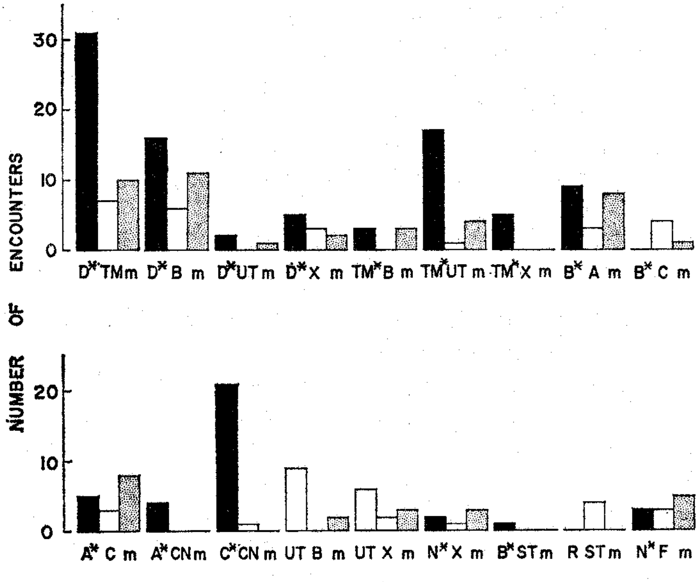


Fig. 16. Initiations of facing-past encounters between neighbouring males in 1968. For each pair of males, encounters could be initiated in three ways: by one or the other male, or mutually (m). Usually that male closest to a mating centre (asterisk, black bar) initiated most of the pair's encounters.

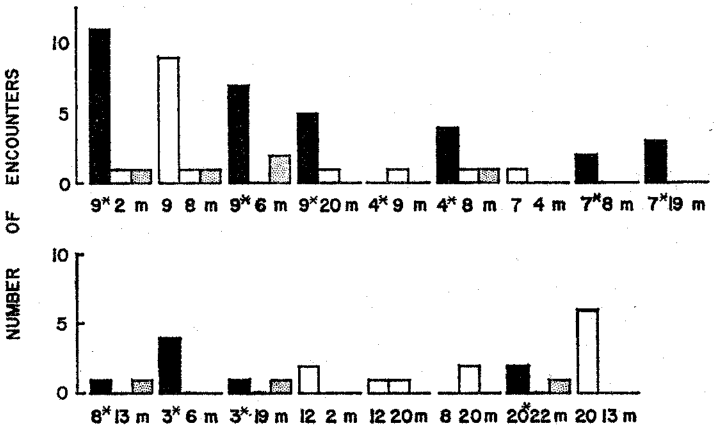


Fig. 17. Initiations of facing-past encounters between neighbouring males in 1969. For explanation see Fig. 16.

even though his neighbour was not near the boundary. Often the neighbour would then walk to join the first male in an encounter. For each pair of neighbours in Figs 16 and 17 the more central one is marked by an asterisk, and the number of encounters which he initiated is represented by a black bar. In 1968 in a series of males progressively farther from the mating centre in male D's territory, the more central of each successive pair tended to start more of the pair's encounters: D started more than B; B more than A; A more than C; and C more than CN. Each male is, therefore, most active along his boundary nearest the pack of females at a mating centre and yet must maintain his farther boundary against gradual encroachments by his more peripheral neighbours.

Later in the morning when females were absent or fewer, patterns in the initiations of facing-past encounters between certain pairs of males tended to equalize. Table XVI compares the initiations of encounters between five pairs of males earlier and later in the morning on days when females were numerous. Male B initiated proportionately more of his encounters with his neighbour, male D, later in the morning than earlier. Thus, in at least one case the tendency for the more central male to initiate a disproportionate number of a pair's encounters did not persist late in the morning. Encounters between males D and TM show the same trend, although in this case the difference is not quite significant. On the other hand, males TM and UT showed the opposite trend: later in the morning the more central male of the pair, male TM, initiated proportionately more of their encounters. In conclusion, polarity in initiations of facing-past encounters seems enhanced, at least between some pairs of territorial neighbours, by the presence of many females at the mating centre soon after sunrise. In spite of these changes in the initiations of facing-past encounters, the zones of encounters usually remained in the same positions throughout each morning and also on mornings when females were few.

D. Termination of Facing-Past Encounters

Rarely does the termination of a facing-past encounter reveal any indication that one opponent has dominated the encounter. Some encounters do result in the retreat of one opponent, but only when one opponent has encroached beyond the usual zone of facing-past encounters into the territory of his neighbour. In this situation, when the resident initiates an encounter, the trespasser ordinarily retreats immediately to the usual boundary zone (Section IX, A). Encounters often shift backwards and

Table XVI. Initiations of Facing-Past Encounters Earlier and Later in the Morning, 27 March to 14 April 1968 (except 3 April)

How encounters were initiated between neighbouring males		Time		χ^2 (Yates correction)	*P*
		Earlier than 1 hr after sunrise	Later than 1 hr after sunrise		
1	D → B	14	2	5·97	<0·02
	B → D*	0	3		
2	TM → UT	5	12	4·02	<0·05
	UT → TM	4	0		
3	D → TM	27	4	3·33	>0·05
	TM → D	4	4		
4	B → A	5	4	0·41	>0·05
	A → B	1	1		
5	A → C	3	2	0·89	>0·05
	C → A	0	3		
6	C → CN	16	4	0·40	>0·05
	CN → C	0	1		
3–6	Combined	51	14	8·23	<0·01
		5	9		

*Data for the interaction of males B and D pertain to the period before male TM's disappearance on 8 April.

forwards over a distance of 1 m or less as the opponents alternately advance and retreat.

A facing-past encounter usually ends as one opponent slowly sidles away and finally turns to leave the encounter. Often, however, the opponent will lunge toward the disengaging male. When this happens, the latter immediately returns to the encounter. Often a male tries to disengage himself from an encounter several times before actually succeeding. A termination finally succeeds when one male manages to turn completely away from the encounter without his opponent starting toward him. Both males then return toward the centres of their own territories. Particularly when both opponents had females within or near their own territories, their encounters tended to terminate quickly, as both males nearly simultaneously disengaged themselves. I classified a termination as mutual if both opponents turned away at approximately the same instant.

The male initiating an encounter usually terminates it. Of 145 encounters in 1968 without mutual terminations, the initiating male terminated 86 per cent. Of sixty-one such encounters in 1969, 67 per cent were terminated by the initiating male. Among certain pairs of males the more central male tended to terminate even those encounters initiated by his more peripheral neighbour. Table XVII includes the data from encounters between males D and TM in 1968 and encounters between male 9 and his more peripheral neighbours in 1969. In both cases the more central males, male D and male 9, terminated more of the encounters initiated by peripheral neighbours than expected. In these two cases the more central male terminated even more encounters than he initiated. This tendency for the more central male to terminate most of a pair's encounters probably stems again from his greater proximity to females. Males near females appear strongly motivated to resume strutting around the females, an interpretation suggested both by their tendency to terminate their facing-past encounters and by their concomitant tendency to have brief encounters (Section VIII, B).

Table XVII. Termination of Facing-Past Encounters Between Neighbouring Males

				χ^2 (Yates correction)*	P
	D	TM	m		
D	29	1	0	6·81	<0·01
TM	3	3	1		
m	4	3	1		
	More central	More periph.	m		
More central**	41	3	4	8·36	<0·01
More periph.	5	7	3		
m	20	10	0		
	9	Periph. neighbour	m		
9	24	3	5	6·72	<0·01
Periph. neighbour†	3	0	0		
m	3	1	0		

In each of the three sub-tables encounters are classified according to initiating male (rows) and terminating male (columns). More central males tend to terminate encounters, even ones initiated by their more peripheral neighbours.

* H_o = the more central neighbour (C) terminates encounters begun by the more peripheral neighbour (P) in the same proportion that P terminates encounters begun by C.

**This table includes all encounters between males TM and UT, A and C, B and A, D and B, D and X, 1968.

† Includes males 2, 6, 8, and 20 in 1969.

Table XVIII. Relationships between Proximity to Females and Three Measures of Male Behaviour: Rates of Strutting; Time Spent in Strutting Posture; and Time Spent in Facing-Past Encounters

	Struts/6 min						
	0–9	10–19	20–29	30–39	40†	N	
T	2	0	6	63	29	51	
N	8	28	28	31	5	36	
O	72	18	7	3	0	66	
	Amount of time in strutting posture (% of 6-min)						
	0–20	21–40	41–60	61–80	81–100	N	Means
T	2	0	0	4	94	51	91·7
N	9	3	14	14	61	36	75·4
O	58	14	13	8	8	66	26·0
	Amount of time in facing-past encounters (% of 6-min)						
	0–20	21–40	41–60	61–80	81–100	N	Means
T	96	2	0	0	2	51	4·9
N	72	11	12	0	6	36	16·7
O	44	14	14	2	27	66	38·4

Figures in the tables indicate percentages of the total number of samples (=N). Columns represent different rates of strutting or different amounts of time. Rows represent different proximities to females (T, females within the male's territory; N, females within 10 m in a neighbouring territory; O, no nearby females).

E. Allocation of Time to Strutting and Facing-Past Encounters

Owing to their briefer facing-past encounters, males with females in their territory devoted much less time to facing-past encounters than did males with no females nearby (Table XVIII). Males with females in their territories spent 92 per cent of their time in strutting posture and only 5 per cent in facing-past encounters. In comparison, when no females were within 10 m, males spent only 26 per cent of their time in strutting posture and 38 per cent in facing-past encounters. Other activities of males near females included chasing intruders (Section IX, J) and mating. Males farther from females also chased intruders. Together mating and chasing intruders never accounted for more than 2 per cent of a male's time. When not strutting or engaged in facing-past encounters, males with no females nearby (situation O) rested in their territories in semi-relaxed or relaxed posture. These two postures, therefore, occupied about one-third of their total time.

Male D, the most successful breeder, often had females in his territory until late in the morning, while other males only occasionally had females in their territories (Fig. 18). Male D and other males established near the mating centre, therefore, spent far more time strutting each morning than did more peripheral males. My data from time-lapse films, however, probably underestimates the amount of time that peripheral males spend strutting, since I usually could not begin filming until most of the females had arrived and concentrated near the mating centre. Earlier, the arriving females are more scattered on the lek, and peripheral males strut more persistently. However, the more persistent strutting by peripheral males around dawn might not stem entirely from greater chances of

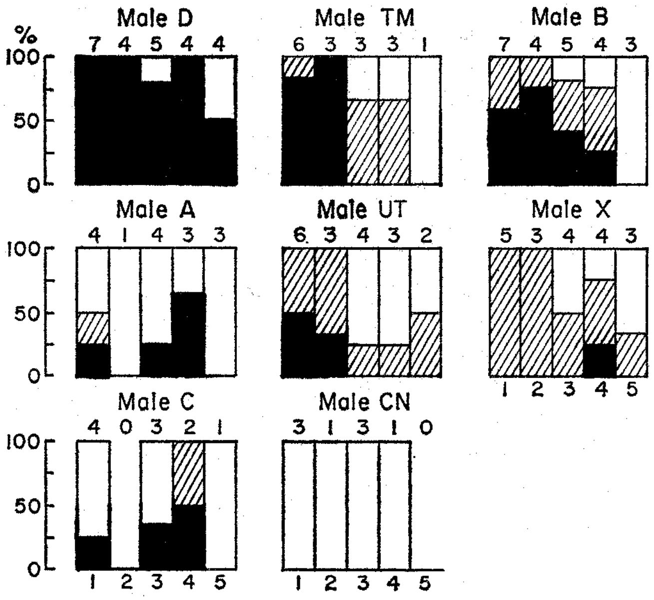


Fig. 18. Percentages of samples in which individual males were at various distances from females. Abscissa is divided into five ½-hr intervals (I–V) beginning 10 min before sunrise. Ordinate indicates percentage of samples (*N* is given above each column) in which the male either had females in his territory (black part of bar), had females within 10 m in a neighbouring territory (hatched part), or had no females nearby (open part). Data from 27 March to 1 April 1968. Males near a mating centre (D, TM, and B) associate with females more often than do other males.

having a female nearby. The quacking call of flying females seemed on many occasions to stimulate strutting. Nevertheless, as the females congregate near the mating centre shortly after sunrise, peripheral males strut much less persistently, whereas males near the mating centre strut steadily as long as females remain, sometimes more than 2 hr after sunrise.

F. Shifts in the Positions of Mating Centres

Further indication of the attraction that a pack of females has for the males comes from two occasions in which the predominant breeder shifted his boundaries slightly to follow short moves of the mating centre (Section VI). In 1968 when the mating centre drifted south-west 8 m, male D accompanied it. At first the mating centre shifted its place each morning, and male D's territory included the entire scope of the movement (Map 4). Then on 31 March and 1 April as the female pack shifted, male D's encounters with his neighbours TM and B also shifted. On subsequent mornings the females gathered initially in the area in which they had ended on previous mornings, and males D, TM, and B also encountered each other in the zone that they had used late in the mornings of 31 March and 1 April. Thus, as the pack of females changed its behaviour, male D simultaneously surrendered a portion of his original territory to his neighbours TM and B. He did not displace any male, because he had no immediate neighbour to the south, where a depression in the surface of the ground appeared unsuitable for strutting males. After the move, just as before, male D continued to predominate in mating.

In 1967 the pack of females also changed their position, as already described in Section VI. Again the predominant breeder, male A, accompanied the pack of females. Presumably the pack of females and male A changed their positions when I erected my blind 10 m from the mating centre. In the afternoon of 11 April and on the morning of 12 April after the females had left, male A visited his presumed original territory 10 m to the south-west of the northern site and encountered neighbouring males there (Map 1). Eventually the pack of females moved to this south-western site, and male A no longer visited the northern site farther from my blind. In my films from 11 April, when the females gathered in the northern area, the durations and intensities of facing-past encounters and wing-fighting among males near the females seemed unusually great. Thus the displacement of the mating centre and male A apparently increased antagonism among the males. Scott (1942) observed a similar increase in antagonism among males when a mating centre moved temporarily to avoid a snow-drift.

To recapitulate, in both 1967 and 1968 the predominant breeder accompanied a shift in the position of a mating centre. In both years the changes in the males' behaviour and in the females' behaviour occurred simultaneously. In 1967 when the move probably resulted from my disturbance of the mating centre, the move appeared to increase antagonism among the males. In 1968 when the mating centre shifted apparently without disturbance from me, no unusual antagonism was noticed. The predominant mater, male D, effectively surrendered a section of his original territory and did not encroach upon any neighbours' territories.

G. Strutting Away from a Lek

I saw this behaviour in two situations: (a) after males had followed females away from the lek early in the season in 1968, and (b) after an eagle had flushed the birds from a lek and a group of females with a number of males landed several hundred metres away in the prairie. I never saw matings in these situations, and females generally showed little sign of precopulatory behaviour.

Females first appear on leks early in the season in loose, wandering groups (Section VIII, A). The strutting males approached as closely as possible to these drifting groups of females, usually without intruding far into neighbouring territories. Males at the edge of a lek, however, sometimes followed a flock of females as it wandered away from the lek. On one occasion, after the peripheral males on the Fords Creek Lek had left their positions to follow a group of females, more central males also left. Eventually many of the males had moved away from the lek in order to continue strutting near the dispersed group of females. These males spaced themselves 5 to 20 m apart and occasionally encountered each other. Usually, though, the males near the centre of the lek did not follow these loose flocks of females beyond their territories. Lumsden (1968) watched several males that followed a group of females beyond the edge of a lek but retained their approximate positions relative to one another. Strutting around females away from any lek also occasionally occurs in winter flocks (Patterson 1952).

H. Reoccupation of Vacancies

Striking polarity in males' territorial interactions appeared again in the reoccupation of the occasional vacancies that arise when territorial males disappear. Such vacancies were allocated to more peripheral males, males less successful in mating than the original occupant. In 1967 one male disappeared: the predominant breeder, male A. In 1968 a series of three disappearances occurred on the Fords Creek Lek: males TM, C, and finally CN. In 1969 only one male disappeared, one originally near my blind.

In 1967 male A failed to appear on the morning of 18 April (Maps 1 and 2), but male N, who was eventually to occupy the entire area vacated by A, did not immediately move into the vacated territory. On the first morning male N only briefly entered A's former area. Late in the morning male N once chased an intruding male across the vacated area. The following morning, 19 April, male N strutted for several short periods in the centre of male A's former territory but still centred his activity to the north-west in his own original territory. On subsequent mornings male N spent progressively more of his time in male A's original area and eventually mated there several times. Male A originally had three other neighbours, males C, S, and SE, none of which extended their territories to include a part of the vacated area. Male C also mated frequently, and the packs of females usually extended into his territory. Male N succeeded in appropriating the entire vacated area without unusual amounts of antagonism with his new neighbours. He did meet male S once on the first morning of male A's absence, but he did not encounter male SE in a position at the east edge of male A's original territory until the following day. Male N had encountered male SE in other positions prior to male A's disappearance, however.

In 1968 a series of three disappearances occurred on the Fords Creek Lek. The vacant territories were eventually appropriated with boundaries essentially intact by males B, CN, and a yearling, respectively. After absences on 6 and 7 April, I returned on 8 April to find TM gone (Map 7). Male B now encountered one of male TM's original neighbours, UT, in roughly the same positions that TM himself had used. Male B's encounters with male D, however, did not immediately converge on the positions where D had previously encountered TM (Maps 9a, b). On 8 and 9 April male B encountered male D only rarely. D had extended his area northward slightly to include a small portion of TM's area. On 10 April, however, males B and D encountered each other in positions near those in which male D had encountered TM formerly. Male B's neighbour on the far side, male A, did not extend his activities as rapidly as male B did. Male A confined most of his strutting to his original area until 12 April. By 22 April, however, male A was encountering male B 3 to 6 m north of their former zone of facing-past encounters (Maps 10a, b). So male B eventually occupied the territory vacated by TM with boundaries essentially intact, and male A, B's more peripheral neighbour, also moved his boundary closer to the mating centre.

When male C failed to appear on 9 April his more peripheral neighbour, CN, immediately occupied the vacated area and began encountering male A in positions very near those at which male C had encountered male A (Maps 9a, b). Following male CN's disappearance sometime between 15 and 22 April, this area remained vacant for several days until a yearling male (male I) established himself there. This male had no previous territory on the lek (see Section IX, M for more details about first-year males). On 25 April he began encountering male A in approximately the same locations used previously by males C and CN (Maps 10a, b). The vacancy that arose in 1969 when male 16 disappeared was also eventually occupied several days later by a yearling male of unknown provenance.

The allocation of vacancies to more peripheral males implies a sort of stochastic radial migration of territory holders. Vacancies are filled by males moving closer to the mating centre, not by central males enlarging their territories.

I. Mortality on Leks

The disappearance of established territorial males presumably arises through natural mortality. However, deaths rarely occurred on a lek. Golden eagles *Aquila chrysaetos* apparently represent the greatest threat to sage grouse on their leks (Batterson & Morse 1948; Patterson 1952; Lumsden 1968). On eight mornings during the three springs of my study, a golden eagle flew over the lek around sunrise. The eagles seemed to recognize their best strategy in approaching the leks. On those few occasions when I spotted the raptor soon after the grouse did, it had suddenly appeared over the nearest rise and was bearing down on the lek at high speed. It flew only a metre or two above the sagebrush, its swift blackish form obscured by the crepuscular light. The eagle would sometimes almost be over the grouse before they all flushed in a frenzy. The grouse usually returned to the lek within ½ hr of an eagle's raid. Although I never witnessed a kill, the eagles do occasionally succeed. On 3 May 1968 I found the remains of a fully adult male sage grouse on the Muddy Springs Lek. Among the dismembered bones and feathers of the grouse was one rectrice of an immature golden eagle. In 1967 I found the remains of an old kill near the periphery of the Muddy Springs Lek. It was also a fully adult male. The bones and feathers were scattered over several yards, so presumably some mammal was responsible but no tracks remained. In each year I walked over much of the lek I studied, but found no other kills.

One might expect that peripheral males would be most vulnerable to predation on a lek. Surprisingly, both of the kills that I found were fully adult males with long, tapering tail feathers, although yearlings are more likely to occupy peripheral positions. On the other hand, the predominant breeders often showed signs of fatigue during the mating season that might make them more vulnerable to predators when away from the lek. Although the predominant breeder in 1967 did indeed disappear, all of the males that mated frequently in 1968 or 1969 remained during my observations.

J. Expulsion of Intruding Males

Scott (1942) described radial differences in the organization of males around a mating centre as follows: a central core composed of a 'master cock' and a 'sub-cock', which perform most of the matings; arrayed around this central core, three to six 'guard cocks', which chase away intruders but perform very few matings. That the 'guard cocks' show altruism is doubtful, but my observations suggest that the male in a pack of females at a mating centre does react differently to intruding males than do his neighbours. My observations accord with Patterson's (1952) conclusion that most intruders are yearling males. I successfully followed a few that moved to the periphery of the lek and assumed the strutting posture. All had the comparatively stubby tail feathers of yearlings. Scott (1942) apparently mistook these intruding yearlings for males with hormonal abnormalities.

Intruders frequently mingle with the large packs of females that gather at a mating centre early in the mating season. Near the pack of females they always assume relaxed or sleeked postures and, therefore, are less easily distinguished from females than are strutting males. The intruders are larger than females and, when seen from the front, show the white chest typical of males. Because they do not erect the feathers on the side of the neck, no white is visible from the rear and only a little from the side. Thus, an intruder can often escape detection by facing away from the nearest territorial male. An intruder within a dense pack of females becomes very inconspicuous except at close range. When a male has a dense pack of females within his territory, he often overlooks intruders among the females until he approaches to within 2 to 3 m of them.

Once a territorial male detects an intruder, usually when the intruder faces him, a vigorous chase ensues. The territorial male rushes after the intruder, who persistently attempts to circle back to the pack of females. A chase often weaves in and out of the pack of females two or three times, so that the females scatter considerably. If an intruder crosses a territorial boundary during a chase, the chase is continued by the next territorial male. A chase is often propagated through several territories and involves a succession of territorial males. An intruder will fly short distances to avoid being overtaken. Eventually the intruder either regains the cover of the pack of females or finally crosses into the territory of a male that fails to notice his presence immediately. In the latter situation the intruder remains quietly where the chase terminated, usually facing away from his last pursuer's territory. Although such an orientation clearly reduced the intruder's conspicuousness to his previous pursuers, I never saw an intruder actually turn to face away from an approaching male as if to avoid detection. If an intruder gains a position, usually at the periphery of the lek, where he goes unnoticed for several minutes, he gradually assumes the semi-relaxed or, rarely, the strutting posture. On one occasion in 1967 I saw an intruder actually strut twice before the territorial male detected his presence.

Since intruders seem attracted to the large packs of females at a mating centre early in the season, males near a mating centre chase them more frequently. However, the male in whose territory the pack actually congregates often begins fewer chases, since intruders in his territory are camouflaged by the pack of females. Thus Scott's observation seems explained: males near, but not actually in, the mating centre, Scott's 'guard cocks', most often chase intruders.

K. Arrival at the Lek in Early Spring

The behaviour on leks during early spring has not been adequately studied. Available observations suggest that the number of males on a lek increases gradually during late winter and early spring. Sporadic activity by a minority of the males on a lek begins during periods of good weather in November and December (Scott 1942). Apparently in late February and March the number of males attending a lek increases rapidly (Patterson 1952; Dalke et al. 1963). However, during this time severe weather will again reduce activity on the leks (see Lumsden 1968). Apparently during periods when deep snow covers the prairie the grouse must move away from their leks in order to find areas where sagebrush is accessible for feeding. During March 1969 snow inhibited lek activity around Farson, Wyoming. Although I arrived in this area by the middle of March, I recorded no males present on any lek until 28 March, when six males appeared at an accessible lek on a county road west of Farson. I had visited this site early in the mornings of 23 and 25 March but had seen no birds and found no tracks. On the morning of 29 March I observed five males at this lek. Two pairs of males encountered each other in the same positions in which pairs had encountered each other the previous morning. By late April this lek had approximately sixty displaying males.

When I first visited the Dry Sandy Lek on 31 March many males were present and loose groups of females wandered through the lek, especially late in the morning (around 08.00 hours), without any signs of localizing their movements. On 31 March, 1, 2, 4, 5 and 10

April I observed the males in an area 50 to 100 m north of mating centre no. 1. Females first showed signs of clustering at mating centre no. 1 on 1 April. On these days, just preceding and during the first congregations of females at the mating centres, I could detect nothing unusual in the intensity or frequency of the males' agonistic encounters. In the area north of mating centre no. 1 some individually identified males occupied their positions regularly during these early observations. Yet several other males clearly shifted their zones of facing-past encounters. Beginning 6 April I changed my observations to mating centre no. 3, a more convenient place for observations.

Similarly, in 1968 on the Fords Creek Lek several males appeared to occupy stable positions during the days when females were first arriving at the lek. Clustering of females in the territory of male D first appeared on 27 March. As early as 19 March, though, males A, B and C had stabilized their zones of facing-past encounters within less than 3 m of the positions they used until 9 April when male C disappeared.

Although evidence remains incomplete, the males apparently increase their activity and attendance at the lek gradually as the weather improves in early spring. At least some of the older males, but probably not all of them, appear to establish stable zones of facing-past encounters before the females begin to congregate at the mating centres. Yearling males establish positions on a lek later in the season than do older males (Section IX, M).

At the lek west of Farson on the first days following their absence during a period of deep snow, only a few males took their positions. Apparently, a small proportion of the males has higher motivation to attend the lek. Perhaps each year as they grow older males tend to occupy their positions on the lek earlier in the spring and more persistently during bad weather. If the oldest males arrived earliest in the spring, this behaviour should predispose them to obtain centrally located territories.

I have found no mention in the literature that males attend their leks even sporadically during the autumn, although males of other lek-forming species of grouse usually do. Autumn display might allow juvenile males and females to experience a lek for the first time at ages of 3 to 5 months, as well as allowing older males to remain in contact with their leks throughout most of the year.

L. Arrival and Departure in the Morning and Evening

The territorial males arrived each morning singly or in small groups. Many flew directly to their territories; others apparently landed some distance away and walked to their territories. In the evening males first appeared walking from the surrounding sagebrush into the area occupied by the lek. They proceeded slowly and paused frequently to feed and preen. After some of the males had taken their positions and begun to strut, latecomers often flew from the periphery of the lek to their territories. My observations indicated that neighbouring males usually did not arrive together either in the morning or in the evening. Lumsden (1968), however, felt that groups of several neighbouring males usually did arrive and depart together each morning. Occasionally a male walking to his territory would have to cross territories already occupied by earlier arrivals. In such situations the trespassing male would adopt relaxed or sleeked posture, detour around the resident, and run if necessary to avoid him. Arriving males, at least during the evening, occasionally strutted in the prairie around the lek. However, once well within the area occupied by the lek, the males did not strut until they reached their territories. I never recorded an arriving male within the lek that challenged another male or strutted except within his own territory.

In late April 1969 the yearling males recently established around the periphery of the lek near my blind arrived 10 to 15 min later each morning than the older males.

After the females have left and the activity of males has decreased, the males begin to leave, again usually singly or in small groups. Occasionally large groups of twenty to fifty males flew away together from a large lek. Some males finally walked away from the lek in small scattered groups. Although the males departed in numerous groups over a period of ½ hr or more, often most of them flew away in roughly the same direction; the direction changed from morning to morning. The males often flew so far from the lek that I could not follow them to the point of landing and so could not determine whether the males ever reassembled after leaving the lek. However, I never saw large flocks of male sage grouse away from the lek during the day in April. Small groups of two to fifteen males were usual.

M. Behaviour of Yearling Males

Except where specified, the preceding sections have dealt only with males 2 or more years old. In contrast, yearling males begin to display regularly later in the season than do older males, occupy less stable positions around the edge of a lek, and rarely if ever mate (Batterson & Morse 1948; Patterson 1952; Eng 1963; Lumsden 1968).

In their first autumn during their post-juvenile moult males acquire the plumage that they will wear during their first spring. This plumage differs only in detail from that of an older male (Section V, E). Although all males reach peak weights between March and May, yearlings average 11 per cent lighter than older males (Dalke et al. 1963) and in addition probably attain maximum weight later in the season (Eng 1963). On the basis of seventy-five males collected in Montana between mid-February and mid-June, Eng (1963) also found that the growth of the yearlings' gonads is delayed in comparison with that of older males (see also Patterson 1952). The average size of the yearlings' testes never reaches the average for older males, although yearlings apparently do produce spermatozoa. They do not normally participate in the mating activities; I never saw one copulate.

At the onset of the mating period yearlings frequently attempt to associate with the pack of females at a mating centre. Probably most of the intruding males in relaxed posture, which often penetrate to the centre of the lek at this stage of the season (Section IX, J), are yearlings. During this early phase of the mating period yearlings strut rarely and then only sporadically for a few minutes at a time in varying positions around the periphery of the lek. During this period they are often chased vigorously by older males established nearby. Map 14 shows where a yearling, male 25, strutted in late April 1969 and the positions in which neighbouring adults encountered him. Clearly, his older neighbours even in late April freely chased him from his favoured positions. As others have also observed (see above), yearlings seem less attached to a particular site on a lek early in the mating period. Dalke et al. (1963) present some evidence from marking studies that the yearling males also show less attachment to a particular lek than do older males.

As the days pass, though, at least some yearling males slowly consolidate their positions at the edge of a lek, positions unoccupied prior to their arrival. Maps 10a, b present the territories of five yearling males (males J, Y, Z, K and I) as they appeared in late April 1968 on the Fords Creek Lek. These yearlings encountered each other in stable zones of facing-past encounters, and three of them successfully established stable zones with their adult neighbours. The yearling male Z encountered his adult neighbour H frequently at their stable boundary. Therefore, by late April a lek has acquired an accretion of yearling males on territories around its periphery. These additional territorial males increase the number of displaying males at a lek approximately halfway through the mating period. On the Fords Creek Lek in 1968 the regular attendance of yearling males increased the number of males on the lek beginning about 10 April (Fig. 1). Other observers have recorded similar increases in the number of males displaying at leks, owing to the increment of yearling males (Batterson & Morse 1948; Patterson 1952; Eng

1963; Dalke et al. 1963).

The displays of yearling males change appreciably as the season advances. In late March and early April in Montana in 1968 I occasionally observed yearling males strutting at the periphery of the Fords Creek Lek. These birds had noticeably smaller chest sacs, and the internal timing of their struts was quicker. In a few instances I recorded individuals that lifted their chest sac three times, instead of the usual two times, before the final, sudden ballooning of the sac. Furthermore, the sound produced during the final sac throw lacked the peculiar resonance typical of the displays of older males, as Lumsden (1968) also noted. In contrast, by 22 April a number of yearling males had chest sacs essentially indistinguishable from those of older males. In spite of this, yearlings never produced the full resonant quality of the older males' struts. In late April 1969 the yearlings on peripheral territories tended to arrive 10 to 15 min later in the morning than did the older males around the mating centre.

To compare the frequencies of strutting by yearling and older males in the absence of females, I used eight 6-min sequences of time-lapse film from the Fords Creek Lek on several days in late April 1968 (Fig. 19). Yearling males tended to strut somewhat more often when no females were nearby than did older males in similar circumstances. Their rates of strutting, however, never reached the high rates typical of older males with females in or near their territories. A yearling male rarely has a female in or near his territory, so I obtained almost no data for these situations. Yearlings spent somewhat less of their time in facing-past encounters than did older males with no females nearby (Fig. 20).

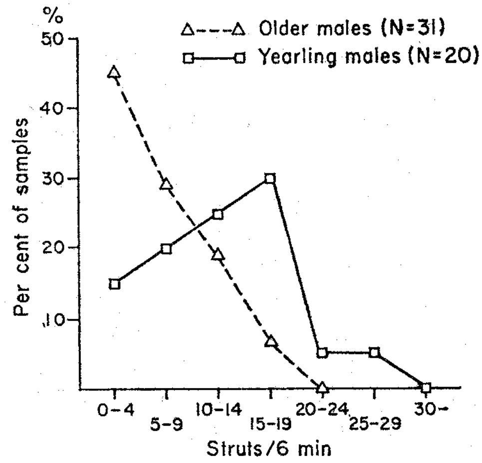


Fig. 19. Rates of strutting among yearling and older males, when no females were nearby. 22 to 25 April 1968.

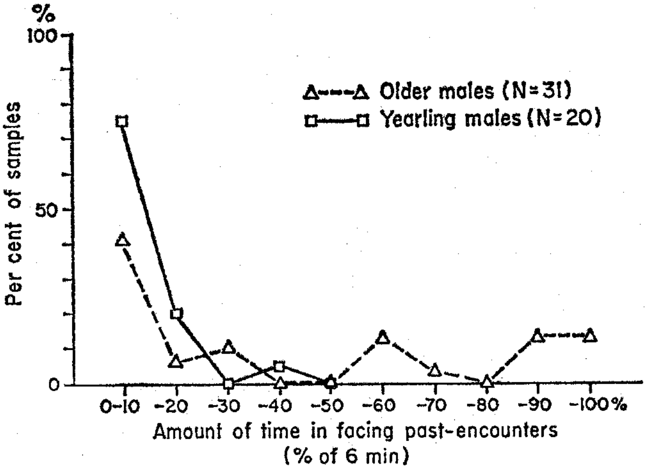


Fig. 20. Allocation of time to facing-past encounters by yearling and older males. 22 to 25 April 1968.

To recapitulate, yearling males begin displaying regularly on a lek later in the season than do older males. They were never seen copulating, although at least some of them eventually establish territories around the periphery of a lek. After establishing a territory their activity patterns resemble those of older males with no females nearby.

X. SUCCESS IN MATING: AN ONTOGENETIC HYPOTHESIS

Territoriality among male sage grouse includes two dynamic features: (1) many yearling males establish territories near the edge of a lek; and (2) the territorial adults during any one season tend to move their positions centripetally as vacancies arise toward a mating centre.

These two observations suggest a mechanism by which a male might come to occupy a territory at a mating centre. If males tend to return to the same lek in successive years and to occupy positions at least as near a mating centre as in the previous season, then an individual male in the course of several years might well reach a position in or near a mating centre.

Direct confirmation of this mechanism would require a marked population of sage grouse. In order to evaluate a negative result, the grouse should not be disturbed on their leks, since Lumsden (1968) and Dalke et al. (1963) both record disturbances in the behaviour of grouse at a lek after cannon-netting. Nevertheless, observations of marked birds by Dalke et al. (1963) do suggest that most males return to the same lek in successive years and that some males return to nearly the same positions on their leks. Lumsden (1968: p. 27) observed three banded males that had returned to approximately the same positions on a lek in two successive years.

The number of years required for a male to reach a mating centre would depend on the annual mortality of males, which would determine the frequency of vacancies on a lek. No good estimates of annual mortality are available for sage grouse. Some rough calculations based on the age distribution of birds trapped during July and August in western Wyoming (June 1963) suggest that mortality among males of at least 1 year of age approximates 50 per cent per year (Table XIX). Males in their second year perhaps have higher mortality than those in their third and fourth years, but this evidence is not clear. Studies by Dalke et al. (1963) suggest mortality rates even higher than 50 per cent a year, on the basis of the low percentages of banded birds returning the following year. Dalke did not separate his data by sex and age-class, however, and it remains uncertain whether trapping and marking birds on their leks might increase mortality or emigration.

Table XIX. Estimated Average Annual Mortality of Sage Grouse After Their First Year Based on the Ages of Grouse Trapped During July and August, 1957 to 1962, Near Farson, Wyoming (June 1963)

Year	Total no. of yearlings and adults trapped		Estimated annual mortality*	
	Males	Females	Males	Females
1957	71	16	0·46	0·25
1958	96	130	0·51	0·31
1959	134	169	0·51	0·34
1960	35	57	0·54	0·33
1961	55	97	0·48	0·67
1962	60	58	0·75	0·52
		Averages=	0·52	0·40

*Calculated as follows: Let N_1 = no. of yearlings (approximately 13 to 14 months old) trapped, N_2 = no. of older birds trapped, s = estimated average annual survival rate, m = estimated average annual mortality rate. Then $N_2 = sN_1 + sN_2$, $1\text{-}m = s = N_2/(N_1 + N_2)$ These estimates assume constant annual mortality rates after 1 year of age, stable age structure in the population, and unbiased sampling of the N_1/N_2 ratio.

Estimates of mortality are available for several other tetraonids (Table XX). For instance, mortality rates among colour-banded blue grouse *Dendragapus obscurus* range from 25 to 31 per cent per year in unhunted populations on Vancouver Island (Bendell & Elliot 1967; Zwickel & Bendell 1967), while in a hunted population in Alberta the rate is 56 per cent per year (Boag 1966). Bendell & Elliot (1967) found no significant differences between the mortality rates of yearling and older males or between males and females.

With a mortality rate of 25 to 50 per cent per year, transposition of a surviving male into a mating centre might require only a few years. This mechanism implies that the more central

Table XX. Estimates of Annual Adult Mortality Rates in Grouse and Pheasants Based on Studies of Banded Populations

Species (location)	Hunting	Annual adult mortality* (%)	Mortality in second year of life compared with later	Sexes differ	References
Red grouse, *L. lagopus* (Scotland)	+	65	Same	No	Jenkins, Watson, Miller (1967)
White-tailed ptarmigan, *Lagopus leucurus* (Montana)	—	29	?	Territorial males perhaps lower = 20%	Choate (1963)
Blue grouse, *Dendragapus obscurus* (Vancouver I.)	—	26–31	Same	No	Bendell & Elliott (1967)
(Alberta)	+	56	Same	No	Boag (1966)
Ruffed grouse, *Bonasa umbellus* (Minnesota)	†	50–60	Same	Females slightly higher than males	Gullion & Marshall (1968)
Capercaillie, *Tetrao urogallus* (Finland)	+	40	?	?	Helminen (1963)
Black grouse, *Lyrurus tetrix* (Finland)	+	80	?	?	Helminen (1963)
Ring-necked pheasant, *Phasianus* (Wisconsin)	?	50–80	?	?	Hickey (1955) Farner (1955)

*Annual mortality of birds after the first year of life.
†In hunted areas mortality slightly higher than in protected areas.

males, those most successful in mating, tend to be the older males. Owing to irregularities in the organization of the leks and the random nature of most mortality, it is difficult without long-term marking studies, to judge exactly how strongly correlated age and mating success in fact are.

One result seems clear, however: yearling males essentially never copulate, although virtually all yearling females breed (Section VIII, A). If my hypothesis concerning the centripetal movement of males' territories is correct, 2-year-old males should also perform few or no copulations, although perhaps they are more likely to mate than yearlings are. The probability that a particular male will occupy a territory in a mating centre might increase steadily with his age. Present evidence cannot specify whether this probability approaches 1·0 at some stage.

To recapitulate, my observations suggest that during their life-span males migrate centripetally within a lek as vacancies arise toward the mating centre. Attainment of success in mating would then be an ontogenetic process, which begins when a yearling establishes a territory at the periphery of a lek. The social organization of a sage grouse lek would depend on polarized interactions between males, often of different ages.

XI. TERRITORIALITY AND POLARITY IN THE INTERACTIONS OF MALES

Previous sections have described the nearly exclusive territories of male sage grouse with stable boundary zones in which neighbours encounter each other. Previous observers have also noticed that the males tend to recur in similar positions on successive days (Scott 1942; Patterson 1952; Lumsden 1968). Some of Lumsden's observations on the Fords Creek Lek, however, differ from my own observations at the same lek 3 years later. He felt that neighbouring males did not encounter each other in stable zones and that the areas used by different males for strutting overlapped widely, conclusions that do not conform to my own observations. He also reported less constant localization of female aggregations and a more even distribution of matings among males than I observed. Possibly his use of a cannon-net on this lek disturbed the birds' behaviour, particularly their fidelity to the site where they had been trapped.

In attempting to understand the manifestations of territoriality among male sage grouse, I have found two concepts especially helpful. One of these, the aggression gradient (see Appendix for a note on terminology), is adopted from van den Assem (1967); the other, the isolation gradient, has not had previous use. These two concepts clarify some difficulties in the description of territorial behaviour and thus allow clearer approaches to the behavioural mechanisms underlying territoriality. The following section will explicate these concepts before I apply them to the territories of male sage grouse.

A. The Phenomenology of Territoriality

Traditionally, studies of the spatial dispersion of animals have used two principal concepts, the territory and the home range. A home range is the area encompassing an individual's movements, based either on continuous or repeated observations of identified individuals (Burt 1943; Jewell 1966). Other terms in the literature for instance, activity space (Weeden 1965), refer to the same idea, perhaps most generally termed an individual range. Either an individual's overall movements or the locations in which it engages in any specified activity (for instance, feeding, singing or mating) can serve to determine an individual range. As the time increases during which an individual's movements are mapped, or as the number of plotted positions increases, the area of the individual range will also increase and ordinarily reach an asymptote (Odum & Kuenzler 1955; Altmann & Altmann 1970). Thus an adequate determination of an individual range must specify both the activity and the time interval sampled.

By merely circumscribing an individual's movements within a polygon, the investigator neglects all information about the relative frequencies of the individual's occurrence at various locations within its range. One possible technique for analysing these different intensities of use within the individual's range involves plotting the frequency distribution of an individual's occurrences as a function of radius from the geometrical centre of all its occurrences (Hayne 1949; Dice & Clark 1953; Calhoun & Casby 1958). Provided the animal's use of its individual range is radially symmetrical, this technique generates an accurate activity gradient for the individual. Alternatively, one might plot isoclines for frequencies of occurrence in quadrats, to produce a diagram resembling a topographic map. Such analyses are available for tree sparrows *Spizella arborea* (Weeden 1965) and baboons *Papio cynocephalus* (Altmann & Altmann 1970). Other authors have qualitatively described core or focal areas that receive frequent use (Kaufmann 1962; Jewell 1966).

Determinations of activity gradients require careful attention to sampling intervals. Accuracy in estimating the frequency of any recurring event, such as an individual's occurrence in a given location, will clearly depend on the total time sampled. Furthermore, frequencies of an individual's occurrences in different locations will usually vary with seasonal and diurnal cycles of behaviour, variations that can have important ecological consequences (for example, Stenger & Falls 1959; Weeden 1965; Stefanski 1967; Altmann & Altmann 1970).

Territoriality requires more complex descriptions. The behavioural manifestations of territoriality can include, depending on the species, active expulsion of intruders, agonistic boundary encounters, exclusive occupancy of an area, changes in dominance at different locations, and spatial restriction of movements or advertising behaviour, such as conspicuous postures, loud vocalizations, or scent marking. At least three fundamentally different kinds of observations are involved: individual ranges, as already described, that specify the distributions in space of an animal's activities; an aggression gradient that specifies how the individual's aggressive interactions vary in space; and an isolation gradient that specifies how much different individuals overlap in their use of space. The latter two concepts are introduced in the following sections, with particular attention to their variation among territorial species.

The aggression gradient. Huxley (1934), Tinbergen (1957, 1960), and van den Assem (1967) have inferred that an individual's aggressive tendencies are higher near the centre of its territory, often near the nest, and decline with distance from the centre. The territorial boundary represents the loci at which an individual's tendencies to attack become equal to its tendencies to flee from its neighbours. The decline in an individual's aggressive tendencies with increasing distance from the centre of its territory specifies an aggression gradient (van den Assem 1967).

The shape of an aggression gradient could be estimated from several kinds of observations. At increasing distances from the centre of an individual's territory, an observer might measure either the percentage of encounters in which the individual dominates his neighbours or the frequency and intensity of an individual's attacks on a constrained test individual or a model. These different measures might well yield disparate results, as measures of an individual's tendency to initiate encounters might not correlate with measures of the outcomes of its encounters, and the interactions of two unrestrained individuals might not correspond to the responses of an unrestrained individual to a model or a test individual. In the interactions of two unrestrained individuals, learning might well occur, so that each one's tendency to initiate attacks in any location would become adjusted to its chances of success there. Thus the eventual shape of an individual's aggression gradient would depend on his interactions with habitual neighbours. The present discussion must rely heavily on field observations of unrestrained individuals, so I shall assume that in any location an individual's tendency to attack is reflected by its ability to dominate agonistic encounters there with neighbouring individuals. The aggression gradient is in this case derived from a dominance gradient, rather than from direct measures of individual's tendencies to attack under controlled conditions.

The shape of the dominance gradient of territorial individuals apparently varies in different species. Among bicoloured antbirds *G. bicolor* an individual's success in agonistic encounters drops sharply in a boundary zone that is relatively narrow in comparison with the diameter of the individual's territory (convex* dominance gradient) (Willis 1967). Convex dominance gradients characterize many other territorial species as well, to judge from more qualitative descriptions in the literature (for instance, Tinbergen 1939; Nice 1937; Lack 1943; Nero 1956; Marler 1956). In contrast, among American robins *Turdus migratorius* the proportion of agonistic encounters that an individual dominates declines progressively with distance from a focal area (concave dominance gradient) (Young 1951). Concave aggression gradients might occur in any species wherever an individual's territory failed to abut a neighbouring

* See Appendix for a note on terminology.

territory. In many hole-nesting birds individuals regularly defend only the immediate vicinities of their nests, although the shape of the gradient near the nest is unknown (von Haartman 1956). Among birds dominance gradients probably vary continuously both in their convexity and their rate of decline with distance from the territory centre.

In some species territorial aggression is only released when intruding conspecifics engage in specific activities, or otherwise provide particular stimuli. For instance, Tinbergen (1939) describes how male snow buntings *Plectrophenax nivalis* ordinarily attack intruding males only when the latter sing. In many sexually dimorphic species, territorial males attack only males, and females attack other females. In monomorphic species, males ordinarily do not attack their mates once the pair-bond has formed but continue to attack alien females as well as other males (for example, Conder 1956; Tinbergen 1960). Several species of birds defend group territories: here a number of individuals accept each other inside the territory (Davis 1942; Carrick 1963; Brown 1963, Hatch 1966). In describing an aggression gradient, therefore, one must specify the individuals and the behaviour patterns that release the aggression.

The isolation gradient. The isolation gradient describes the movements of conspecific individuals with respect to the area inhabited by a given individual. One suitable measure of isolation is the frequency of the resident's occurrence at a given location in relation to the frequency of occurrence of other, conspecific individuals there. This ratio, when expressed as a function of location, would specify the resident's isolation gradient.

An isolation gradient is thus the obverse of a home range, or individual range (see above), which denotes the area encompassing an individual's movements. The isolation gradient reflects instead how much neighbouring individuals' movements overlap in space and, therefore, specifies the extent to which an individual exclusively occupies, or monopolizes (Jewell 1966), some area.

Like an aggression gradient, an isolation gradient for any territorial resident pertains to a specific class of other individuals. In many birds a territorial male's isolation gradient with respect to females or immature individuals would differ considerably from that with respect to other adult males. In this paper, both the aggression and isolation gradients of territorial male sage grouse will refer to relationships with other territorial males.

Isolation gradients could pertain to specific activities rather than to mere presence regardless of the type of activity. For genetic or ecological analyses, isolation gradients specific to mating or feeding behaviour might become necessary. For sage grouse, I shall use the previously stated definition of an isolation gradient, based on the relative frequencies with which the resident and other territorial males occupy a given area, regardless of their activities there. As described below, trespassing male sage grouse are in fact usually strutting.

To assess the exclusiveness with which an individual occupies a given location, one must estimate frequencies of occurrence there for a number of individuals. Just as in determinations of activity gradients, the time periods sampled require careful choice. Accuracy in estimating a resident's isolation at any one location will ordinarily increase as the total time sampled increases. Owing to short-term cycles in individuals' movements and short-term effects of individuals' interactions, estimates of a resident's isolation at any location in short time intervals would vary considerably. As the time period for each sample increases, the variation among sample means will decrease toward an asymptote. The exclusiveness of an individual's occupation of space is then best expressed by such long-term estimates of isolation as a function of location.

The exclusiveness of an individual's access to some renewable resource will depend both on the individual's isolation gradient and on the rate at which the resource regenerates. For a rapidly renewing resource, isolation ratios determined in short time intervals would appropriately indicate the extent to which individuals had exclusive access to the resource at any one site. A more slowly replenished resource would require longer intervals to assess a relevant measure of isolation.

Species differences in isolation gradients arise in part because the limitations on individual's movements include both spatial and temporal dispersion, and the relative importances of these constraints vary with the species. Among feral house cats (Leyhausen & Wolff 1959), individuals' ranges overlap widely, so the long-term asymptotic measures of an individual's isolation would be low at all locations over a large area. Because at any location individuals maintain some minimal separation in time, over short time intervals an individual's isolation would always be high. Thus over relatively large areas isolation among individuals is principally temporal. By contrast, among breeding song sparrows, to cite a classically territorial species, over a relatively long time period isolation is principally spatial. At all locations within some relatively large area, the asymptotic measures of an individual's isolation would be high. Only at the boundary between two song sparrows' territories would they have long-term isolation ratios as low as those obtaining for house cats over most of their home ranges.

Although long-term measures of isolation might better express the exclusiveness of an individual's territory, short-term changes in the probability of intrusions can illuminate the behavioural mechanisms that regulate the isolation gradient. These behavioural processes acquire special interest when intrusions occur regularly across a defended territorial boundary, a situation encountered in some territorial birds. For instance, male snow buntings and European robins *Erithacus rubecula* on the basis of Tinbergen's (1939) and Lack's (1943) qualitative descriptions, have convex dominance gradients, which decline sharply across territorial boundaries, yet neighbours trespass into each other's territories frequently. Trespassers have cryptic behaviour and usually are expelled only when they begin to sing. Other passerines maintain essentially exclusive territories demarcated by convex dominance gradients. Trespassing was rare in the song sparrow population studied by Nice (1941) and not recorded in the wren-tits *Chamaea fasciata* studied by Erickson (1938). Although trespassing individuals might often escape detection because of their cryptic behaviour, these two thorough studies indicate that in some territorial species trespassing is at least infrequent.

Several mechanisms could explain a lack of congruence in the dominance and isolation gradients of a territory. The resident might regularly fail to detect intruders, when unable to survey the entire scope of his territory from any one place; he might remain preoccupied with some activity incompatible with evicting intruders; or he might perhaps tolerate intruders, unless they engaged in some particular activity. The neighbouring individuals must also have some tendency to leave their own and enter the resident's territory, whether or not contingent upon the resident's preoccupation with other activities or his absence from the vicinity. The isolation gradient is thus not an attribute of one individual; it results from the interactions, past and present, of a resident and his neighbours.

Even when the isolation gradient coincides with the dominance gradient of a territory, interactions of territorial neighbours will determine the shape of the isolation gradient. Exclusion, in other words, a steep isolation gradient, arises both through the resident's expulsion of intruders by overt aggression and through the neighbours' avoidance of the resident's territory. Actually a resident's behaviour often will not allow clear distinctions among attack, threat, and advertisement, nor a trespasser's behaviour allow clear distinctions between defeat and avoidance. The interactions between a territorial resident and his neighbours that determine the moment-to-moment probabilities of intrusion eventually generate the long-term isolation gradient. The isolation gradients of territorial male sage grouse, as described below, clearly depend on such interactions.

A dual approach to the investigation of territoriality. Because the area that an individual occupies exclusively has no necessary relation to the area within which it dominates a majority of its agonistic encounters, Noble's (1939) definition of a territory as 'any defended area' is ambiguous. Defence might imply either exclusive occupancy or expulsion of intruders (Nice 1933), and, while the latter might result in exclusion, exclusion need not require active expulsion. As already mentioned, expulsion and avoidance often constitute inseparable components of exclusion. Further difficulties with Noble's definition arise in those species in which the dominance gradient declines progressively with distance from a focal area (concave dominance gradient), so by the criterion of success in agonistic encounters virtually no area is defended absolutely.

Pitelka (1959) would define a territory as 'an exclusive area, not merely a "defended" one', on the basis that exclusion would constitute the important ecological consequence of territoriality, regardless of how it is achieved. However, an individual might ensure his access to resources without occupying any exclusive area. Agonistic interactions could limit the number of resident individuals in some region, and thereby regulate the overall intensity of resource utilization, without any individual occupying an exclusive domain (Willis 1967).

Rather than pursue a unitary definition of territoriality, I shall consider independently the dominance gradient, the territorial resident's ability to dominate agonistic encounters with its neighbours as a function of location, and the isolation gradient, the resident's use of an area in relation to its use by other territorial males.

B. The Nature of Sage Grouse Territories

The aggression gradient. Encounters between neighbouring male sage grouse apparently establish the locations of boundary zones between territories rather than determine classical dominance–subordinance relationships between opponents. Like the boundary encounters of classically territorial species, the facing-past encounters of male sage grouse are frequent but rarely severe. Furthermore, one opponent does not 'win' and the other 'lose', as encounters, within the usual boundary zone, essentially never result in the displacement or injury of one contestant. When an encounter terminates, both contestants return to their respective territories. The male initiating an encounter usually terminates it. When a strutting male transgresses the boundary zone, he ordinarily quickly retreats to the boundary zone after the resident male initiates an encounter. Within the usual boundary zone, facing-past encounters rarely shift position more than a metre.

First-year males, in contrast, do get chased long distances by neighbouring older males, especially when the yearlings first begin to occupy regular positions around the periphery of the lek. Eventually, though, many yearlings succeed in establishing stable boundary zones with their older neighbours.

Like many other territorial birds, male sage grouse occupy territories separated by narrow, mutually recognized zones, within which neighbours encounter each other as equals. Within his own territory a male sage grouse dominates all other males. Trespassers ordinarily retreat to the boundary zone when challenged. The dominance relationship of two neighbours reverses within a zone only 1 or 2 m wide. Since each male's capacity to dominante agonistic encounters remains maximal until it decreases steeply in a narrow boundary zone, a territorial male sage grouse has a convex aggression gradient (Fig. 21).

The isolation gradient. Territorial neighbours reciprocated in avoiding frequent or deep intrusions into each other's territories. While on a lek each male usually remained within his own territory. On a few occasions in 1968, I saw several males follow a wandering flock of females away from a small lek. However, I never saw a

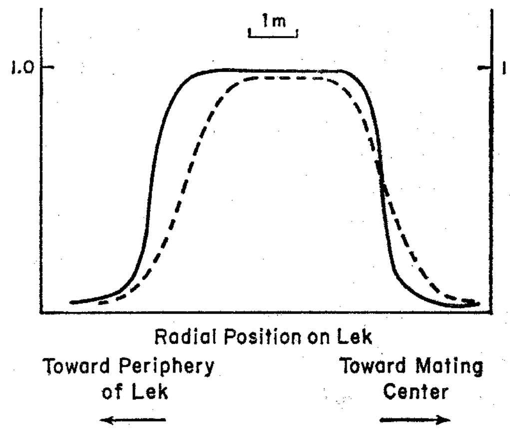


Fig. 21. Estimated aggression and isolation gradients of a sage grouse territory plotted along a radius from the mating centre. Solid line, residents' dominance; broken line, isolation ratio. At each location, the isolation ratio equals the residents' occurrences there divided by the total occurrences there of all territorial males, and the resident's dominance is the proportion of agonistic encounters with neighbours in which his opponent withdraws.

male move strutting across a neighbour's territory unless the neighbour himself was also following the females away from the lek. A peripheral male could copulate within his territory with the same security that a central male enjoyed, since males never intruded more than a short distance into neighbour's territories to interrupt their matings.

When a large pack of females gathered on a lek each male tended to concentrate his strutting on the side of his territory nearest the females. Occasionally in these circumstances a strutting male would encroach into his neighbour's territory beyond the zone of facing-past encounters. These intrusions rarely exceeded 1 m and usually persisted only until the regular occupant of the territory initiated a facing-past encounter. The isolation gradient of a male's territory is thus not symmetrical. Intrusions are somewhat more likely on the more peripheral boundary than on the more central boundary (Fig. 21). Because male sage grouse occasionally encroach beyond their boundary zones in which neighbours meet as equals in facing-past encounters, the isolation gradient of a male's territory does not decrease quite so abruptly as the dominance gradient (Fig. 21).

The interactions of territorial neighbours determine the slopes of their isolation gradients. To some extent, the exclusiveness of a male sage grouse's territory is assured by his active expulsion of intruding males, both his neighbours and the intruding yearling males (Section IX, M). Usually neighbours encroach beyond their territorial boundaries, as defined by their dominance gradients, when the resident is preoccupied with mating or strutting near females (Sections VII, C and IX, A). Yet internal inhibitions against intrusion are also indicated. Matings are interrupted only when they occur near a territorial boundary. Vacancies sometimes remain unoccupied for 1 or 2 days after the disappearance of the original occupant. On arrival each morning or evening the males proceed to their own territories and do not occupy the areas temporarily left vacant by late arrivals. Thus in spite of the attraction of the mating centre for the males, each male also retains an attachment to his own territory and a concomitant inhibition against intrusions into others' territories. The isolation gradient depends on the balance between a resident's capacity to expel intruders and the attachment of his neighbours to their own territories.

Polarized territoriality. The behaviour of male sage grouse conforms in many respects to the classical pattern of territoriality. Nevertheless, their territoriality diverges from the classical conception in having certain polarized, or nonreciprocal, features, as well as reciprocal features (see Section II, A). The interactions of territorial males nearer a mating centre with those farther away lack reciprocity in the initiation and termination of facing-past encounters between neighbours and in the occupation of vacancies. In all these cases, the polarized interactions of radial neighbours apparently originate in the attractiveness of the mating centre for the territorial males. Territorial males nearer a mating centre evidently inhibit the occupation of these areas by males established in more peripheral positions. In effect, the territories themselves show hierarchical ranking.

Furthermore, the behaviour of males nearer a mating centre differs in several respects from the behaviour of those farther away. Because the more central males have females within or near their territories for a greater proportion of each morning, they perform most of the matings, strut during a greater proportion of the morning, and engage in briefer facing-past encounters. The males nearer a mating centre also usually occupy smaller territories.

From a cursory examination of data on facing-past encounters it appeared that lateral territorial neighbours, in contrast to radial neighbours, initiate encounters with one another more or less equally. However, the territories of lateral neighbours are usually not exactly equal in distance from the nearest mating centre, so interactions between lateral neighbours are less easy to interpret than those between radial neighbours.

Lumsden (1968) has suggested that male sage grouse might maintain hierarchical ranking throughout the year, away from their lek as well as on their lek. Like Lumsden I noticed no higher levels of agonistic activity early in the season than later, which suggests that the males' relationships either stabilized soon after arrival in the spring or that their relationships were remembered from earlier occasions. However, I could not confirm his conclusion that the males arrived and left together each morning (Section IX, L), so I feel uncertain whether the males around each mating centre remain together when away from the lek. Winter flocks often include over a hundred birds, a number that might preclude the formation of hierarchies based on individual recognition.

The following tabulation will recapitulate the indications of reciprocity and polarity in the relationships of territorial male sage grouse. Reciprocity is indicated by the following observations:

(1) stable boundary zones within which agonistic encounters between neighbouring territorial males occur;
(2) minor degree of intrusion into neighbouring territories and prompt retreat of trespassing males when challenged;
(3) encounters in the boundary zone lack polarized results.

Hierarchical organization of the territories results from two sorts of polarities in the males' territorial behaviour: (1) non-reciprocal interactions; and (2) differences in the behaviour of males related to the positions of their territories and hence to their proximities to a mating centre. Non-reciprocal interactions include the following:

(1) allocation of vacancies to more peripheral neighbours;
(2) males tend to initiate and terminate most of their facing-past encounters with their more peripheral neighbours.

In comparison with males farther away, males in or near a mating centre:

(1) strut more;
(2) devote less time to facing-past encounters;
(3) hold smaller territories;
(4) copulate more frequently.

Polarities in the behaviour of territorial male sage grouse all hinge on the attraction of territorial males toward the mating centre where females gather. The polarized interactions of neighbouring territorial males generate a radially organized, hierarchical social structure.

Determination of territory sizes. The sizes of the territories on a lek, as demarcated by the zones of facing-past encounters, relate roughly to the males' successes in mating. More peripheral territories are often, although not always, larger, and matings rarely occur there. Territories nearer a mating centre are usually among the smallest territories, and in some of these mating is frequent (Section IX, A).

In some species territory size correlates with the aggressiveness of the resident individuals. For instance, van den Assem (1967) found that male three-spined sticklebacks in larger territories initiated most of their encounters with their neighbours in smaller territories. Among red grouse Watson (1967) reported that territory size correlated with an index of aggression that depended on the frequency of the resident male's aggressive encounters and on the male's success in encounters. Watson (1964) does not describe his criteria for determining success in an encounter, so his results are difficult to compare with my own.

Among male sage grouse differences in territory size probably correlate roughly with differences in the amount of time allocated to boundary encounters, one possible measure of a male's aggressiveness. Male sage grouse with territories near a mating centre have females in or near their territories most of each morning during the mating period. When females are nearby, males engage in much briefer facing-past encounters, yet increase the frequency of their encounters relatively little. Therefore, males near females spend less time encountering their neighbours than they do when no females are nearby. Although more central neighbours initiate most of their facing-past encounters with more peripheral neighbours, they also terminate most of the encounters, apparently because males with females in their territories are strongly motivated to continue strutting near the females. Thus males established near a mating centre devote less time in the course of a morning to agonistic encounters, and their territory sizes are usually among the smallest on the lek.

The effect of a territorial male's preoccupation with females inside his territory became especially apparent when females remained in a territory away from the usual mating centre. On these infrequent occasions, neighbouring males would encounter the territory occupant inside the usual zone of facing-past encounters, thus compressing the territory in which the females remained. Such situations occurred temporarily on 14 April 1968 when males X and UT encroached on male N's territory and on 23 April 1969 when male 8 moved into the territories of males 9 and 20 (Section IX, A; Maps 9a, b and 13).

Territories at a mating centre, on the other hand, did not change size depending on the presence or absence of females at the mating centre. The habitual presence of females in these territories might have a cumulative effect on territorial boundaries that would eventually persist regardless of the females' presence.

The territorial resident's behaviour does not alone determine the location of his boundaries, however. Instead, the size of a territory results from an interaction of: (1) internal resistance exerted by the territorial resident, and (2) external pressure applied by territorial neighbours. As already discussed, the efficiency of the internal resistance exerted by more central males might not equal that of more peripheral males. Furthermore, external pressure on central territories might be greater than on more peripheral ones. When females congregate at a mating centre, the boundaries of the central males' territories come under increased pressure as their more peripheral neighbours tend to encroach slightly toward the females (Section IX, C). If the attraction of the mating centre for territorial males decreased at increasing distances, males established at greater distances from the mating centre might well exert less pressure on their more central neighbours.

Precedence among peripheral neighbours in the occupation of vacancies. The reoccupation of vacancies on a lek presents an unresolved problem. Which of two neighbours equally distant from a mating centre will occupy a vacancy arising closer to the mating centre? In two cases a vacancy had two or more neighbours equally distant from the mating centre. When male TM disappeared in 1968, both male B and male UT appeared equally likely candidates for reoccupation of the vacancy. In 1967 when the predominant mater, male A, disappeared and left a vacancy that included part of a mating centre, his three neighbours males N, SE and S seemed equally likely to reoccupy the vacancy. Male A's fourth neighbour, male C, already occupied a portion of the area in which matings occured frequently. At least in this second case, following the disappearance of male A, none of the three neighbours immediately occupied the vacancy. Not until 3 days later was male N using the vacated area extensively, encountering the other three neighbours frequently and mating there. Contrary to what one might expect, the reoccupation of vacancies was not attended by an increased frequency or intensity of agonistic encounters in which one male obtained an advantage. When male N replaced male A, agonistic encounters occurred infrequently and did not involve wing-fighting. Both in this case and in the case of male TM's disappearance I could not determine what factors predisposed one of the neighbours to reoccupy the vacancy. Perhaps differences in the males' ages would give an advantage to the older. Indeed, male SE in 1967 had slightly less tapering rectrices than male N, perhaps indicating that male SE was the younger of the two (Section V, E).

Individuality in the interactions of males. A male sage grouse on a lek has one clear source of individual identification: his location. When males arrive on a lek in the morning or in the evening, each proceeds to his own territory. A male does not move his position even if his more central neighbour arrives later than he does. The position of a male's small territory identifies his rank in the hierarchy of territorial males.

If male sage grouse on a lek can recognize each other individually on the basis of cues other than territorial location, their interactions reveal little evidence of such recognition. For instance, a male's behaviour changed remarkably little when a former neighbour disappeared and a new neighbour took its place. Usually the zone of facing-past encounters continued in the same locations, as when male N replaced male A in 1967 and when male CN replaced male C in 1968. When male B replaced male TM in 1968 certain changes did follow, though. The boundary with male D at first shifted, although it finally returned approximately to its original position. Although the boundary zone with the other neighbour, male UT, remained unchanged, the behaviour of male UT clearly did change. Prior to the replacement, male TM had initiated most of the facing-past encounters in the boundary zone with male UT, while after the replacement male UT initiated most of the facing-past encounters there (Fig. 16; compare encounters between UT and TM with those between UT and B). No reversal in the patterns of initiating facing-past encounters occurred when male CN replaced male C in the territory adjacent to male A. However, in this case male A had encountered male CN previously in other locations.

Other than their strict localization, territorial male sage grouse do not have clear sources of individual identification. The species apparently has not evolved any feature of plumage or behaviour that would clearly facilitate individual recognition. Their displays and acoustic signals, as a result of extreme species-specific stereotypy, show only slight individual differences among males at least 2 years old. The complex patterns of under-tail covert spots that I used for individual recognition are probably beyond the discriminatory powers of sage grouse. Many other birds do have acoustic signals that clearly identify the individual (Weeden & Falls 1959; Marler 1960; Thorpe 1968; Falls 1969).

Individual recognition is probably not necessary to maintain hierarchical organization among individuals. Instead, individuals might differentiate among classes of other individuals. An individual in a hierarchy only needs to discriminate between other individuals likely to have higher rank and those likely to have lower rank than its own. If rank correlated with aggressive tendencies, then an individual would only have to recognize individuals with higher and lower aggressive tendencies, for instance by their longer or shorter critical distances for initiating an attack, or by their postures (Foreman & Allee 1959).

The rank of a male sage grouse in the hierarchy of territorial males on a lek correlates with the distance of his territory from the mating centre. The hierarchical organization of territorial male sage grouse might thus depend on the spatial localization of individuals rather than on individual recognition independent of location.

XII. LEK MATING SYSTEMS IN OTHER GROUSE

The lek behaviour of sage grouse appears to represent the extreme development of polygyny among grouse. In addition to sage grouse, seven of the sixteen other species of grouse form leks for mating. Almost no information is available about three of these species (*Lyrurus mlokosiewiczi*, *Tetrao urogalloides*, and *Tympanuchus pallidicinctus*). The other four species show many parallels with sage grouse. The communal display grounds occur at traditional sites. A few of the males on each lek perform most of the matings. Individual males maintain small territories defined by zones in which neighbours encounter each other. Yearling males occupy peripheral positions and virtually never mate.

The traditional location of leks is well known for prairie chickens *T. cupido*, sharp-tailed grouse *P. phasianellus*, black grouse *L. tetrix*, and capercaillie *Tetrao urogallus* (Hjorth 1970). In all species the number of males on a lek varies with the season, the locality, and the particular lek. Only a few censuses of lek sizes are available. Capercaillie leks apparently average smaller than leks of the other species. Kirikov (Dementiev & Gladkov 1967) censused two areas that included fifty-six males on six leks and eighteen males on five leks, respectively, or 9·4 and 3·6 males per lek. Most reports of prairie chicken, sharp-tailed grouse, and black grouse leks mention at most thirty to forty males. However, in sparsely inhabited areas of Russia black grouse leks may reach 150 to 200 males (Dementiev & Gladkov 1967), but apparently only in sage grouse are leks of more than fifty males a regular occurrence. In other species I have found no reports of leks with more than 200 males.

Descriptions of the territorial behaviour of males appear in almost all accounts of lek behaviour of these species: black grouse (Lack 1939; Höhn 1953; Kruijt & Hogan 1967; Koivisto 1965; Hjorth 1970); capercaillie (Lumsden 1961; Hjorth 1970); prairie chicken (Hamerstrom 1939; Hamerstrom & Hamerstrom 1955, 1960; Schwartz 1945; Robel 1964); sharp-tailed grouse (Lumsden 1965; Evans 1969; Hjorth 1970). In all species the central territories are usually smaller than more peripheral ones. Territories are smallest in the sharp-tailed grouse, the smallest ones usually being about 20 to 30 m^2 in area (Lumsden 1965; Hjorth 1970). In prairie chickens the smallest territories are about 75 m^2 (Hamerstrom & Hamerstrom 1960). In black grouse the smallest territories that Lack (1939) observed were about 35 m^2. However, Kruijt & Hogan (1967) found none less than 100 m^2 in area, and central territories on leks observed by Hjorth (1970) ranged from 170 to 260 m^2 in area. Capercaillie cocks occupy much larger territories, 50 to 100 m centre-to-centre, with vaguely defined boundaries (Lumsden 1961; Hjorth 1970).

The species differ markedly in the males' attachment to their territories when females visit the lek. Male prairie chickens, sharp-tailed grouse, and capercaillie frequently leave their territories to approach females elsewhere on the lek (Lumsden 1965; Hamerstrom & Hamerstrom 1960; Robel 1964; Hjorth 1970). In contrast, black grouse males, like sage grouse, usually remain within their territories at all times (Höhn 1953; Kruijt & Hogan 1967; Hamerstrom & Hamerstrom 1960; Hjorth 1970).

The expression of territorial behaviour thus takes different forms in the various species of lek-forming grouse. Territorial male black grouse, sage grouse, prairie chickens, and sharp-tailed grouse have convex aggression gradients, while the behaviour of male capercaillies suggests a concave gradient. The territories of male black grouse and sage grouse manifest steep isolation gradients even when females congregate within the lek, whereas in the other three species neighbours trespass frequently when females are present. In all species isolation gradients are probably steepest in the absence of females.

Most copulations are performed by males at least 2 years old who are established near the centre of a lek (Robel 1967; Koivisto 1965;

Kruijt & Hogan 1967; Lumsden 1965). Although Robel (1964, 1966, 1967) reports that male prairie chickens most successful in mating occupy larger territories than less successful males, his measurements of territory size are not comparable with those of other observers. He determined the males' individual ranges (see Section IX, A) on a lek by plotting their positions at 15-min intervals. Other observers have determined territory sizes from the positions of the agonistic encounters between neighbours. On prairie chicken leks the central males, which mate most often, leave their territories to approach females nearby.

Studies of banded males have shown that male prairie chickens, sharp-tailed grouse, and black grouse return to the same lek in successive years (Robel 1967; Hamerstrom & Hamerstrom 1960; Koivisto 1965; Evans 1969; Hjorth 1970) and that males improve their mating success with age (Robel 1967; Koivisto 1965). Evans (1969) confirmed that four surviving male sharp-tailed grouse returned to the same positions on their lek in the following year. A fifth male moved his territory 8 m into the centre of the lek to occupy a vacancy. This observation conforms to my hypothesis that individuals' territories move centripetally on a lek.

Many studies have mentioned the peripheral positions and less constant attendance of yearling males (Lumsden 1961; Lack 1939; Koivisto 1965; Kruijt & Hogan 1967; Robel 1967). Yearling male black grouse penetrate the centre of the lek as intruders (Koivisto 1965; Kruijt & Hogan 1967). Robel (1965, 1967) presents some evidence that yearling male prairie chickens continue displaying on leks later in the spring than do older males. Capercaillie yearlings occupy more peripheral positions and have less developed displays (Dementiev & Gladkov 1967; Lumsden 1961). In addition, Kirikov (reviewed by Dementiev & Gladkov 1967) found that males in their second spring began displaying later than the older males. He found that if all the older males were removed from a lek, the following year 2-year-olds began displaying first but not so early in the season as the older males had. If he removed the 2-year-olds as well, then yearlings occupied the centre of the lek. The seasonal course of display by yearling and older males, and the growth of yearling and older males' testes, needs to be studied in other lek-forming species of grouse.

Autumn display probably occurs in all lek-forming species of grouse. Black grouse in Sweden continue to visit their leks sporadically throughout the winter (Hjorth 1968), as do prairie chickens in Kansas and Oklahoma (Jones 1964).

Although female sage grouse are peculiar in the degree to which they clump together in a small area on the lek, females of other species of lek-forming grouse do show some tendencies in this direction. Female prairie chickens and sharp-tailed grouse tend to concentrate in groups near the centre of a lek within the territories of a few males (Schwartz 1945; Lumsden 1965). Black grouse females, especially during the morning in which they copulate, spend most of their time on the lek within the territories of a few of the males (Kruijt & Hogan 1967). By observing banded females Hamerstrom & Hamerstrom (1955) concluded that female prairie chickens probably copulated once a season after visiting a lek on several mornings.

Estimates of the dispersion of copulations among all the males on a lek are available only for black grouse. At one lek observed by Koivisto (1965) one male in a total of ten performed about 75 per cent (17/24) of observed copulations. On the lek studied by Kruijt & Hogan (1967) in 2 years approximately one-third of the males performed 75 per cent of the matings.

The leks of sage grouse, therefore, reveal almost no unique qualities, although in several respects the behaviour of sage grouse represents the extreme development of lek behaviour among grouse. The leks of sage grouse probably average more males per lek than do leks of any other species. Furthermore, some sage grouse leks have the largest numbers of males reported for any species of lek-forming grouse. The dense packing of females at particular sites within a lek also represents an extreme development of tendencies present in other grouse. Finally, on the basis of available evidence, copulations are probably less evenly distributed among male sage grouse than among males of other species. A smaller proportion of male sage grouse at a lek appear to serve most of the females. In all lek-forming species of grouse, yearling males occupy peripheral positions and essentially never copulate.

XIII. SUMMARY

Section I. Previous work has indicated that sage grouse *Centrocercus urophasianus* practice extreme polygyny (Simon 1940; Scott 1942; Patterson 1952; Lumsden 1968). The behavioural interactions that regulate this mating system have remained unclear, as the males' behaviour suggests both territoriality and dominance hierarchy.

Section II. A basic difference between territorial and hierarchical social systems involves the extent to which the constituent individuals' relationships are polarized, rather than reciprocal. In a dominance hierarchy the interactions between individuals are polarized; territorial individuals typically interact reciprocally. Nevertheless, interactions among territorial individuals can incorporate two kinds of polarity: territorial dominance, as each individual dominates his neighbours inside his own territory but is subordinate to them in their territories; and polarized territoriality, when territorial individuals established in preferred areas prevent other territorial individuals from occupying these areas. The indications of reciprocity and polarity in the interactions of male sage grouse are investigated in this paper to clarify the expression of territoriality and dominance hierarchy in their social organization.

Sections III to VI. Sage grouse gather for mating at communal display grounds, or leks, at traditional sites on sagebrush prairie. Although females arrive for mating primarily during 2 or 3 weeks in late March and April, males usually attend the leks regularly from February or March into May. Every morning and evening and often all night the males occupy small territories (13 to 100 m^2) defined by boundary zones in which neighbours meet for facing-past encounters and wing-fighting (behaviour patterns are described in Section IV). Within their territories males repeatedly perform an elaborate, stereotyped display, the strut.

I studied three leks with different numbers of attending males (154, 30 and 260), one lek each spring from 1967 to 1969. Time-lapse cinematography was used to record the males' positions and activities.

Females congregate in dense packs at certain sites on a lek, usually in the same places on successive mornings. These sites, termed mating centres, also usually remain in the same locations in successive years.

Section VII. Almost all copulations occurred at these mating centres, within the territories of one or two males, although as many as eighty other males occupied territories around each mating centre. Consequently, each year fewer than 10 per cent of the males completed more than 75 per cent of all copulations. Neighbours occasionally interrupt each other's copulations, but usually only those attempted near or within the boundary zone of facing-past encounters. Therefore, a male's success in mating does not depend on direct prevention of copulations by other males. Instead, a male becomes successful in mating by acquiring a territory at a mating centre.

Section VIII. The behaviour of females arriving at a lek suggests how they might locate the mating centre. The possible cues associated with a mating centre are evaluated for their specificity in identifying the position of the mating centre and for their availability to the females. Although the behaviour of males near a mating centre differed in several respects from that of more peripheral males (for instance, the former strutted more persistently and engaged in much briefer and perhaps slightly more frequent facing-past encounters), these differences apparently depended mostly on the males' proximities to females, rather than on intrinsic differences among the individual males. Most males 2 or more years old, whether near a mating centre or not, responded similarly to the presence of females within their territories.

Since a mating centre ordinarily has a traditional location within a lek, females might learn its position. Only limited guidance could come from the generally smaller territories of males near a mating centre.

Section IX. Reciprocal interactions among males included the limited scope of neighbours' intrusions into each other's territories and neighbours' encounters as equals in boundary zones between their territories. Non-reciprocal, or polarized, relationships resulted from the attraction of males toward a mating centre. Since their more peripheral neighbours tended to encroach beyond their boundary zones, towards the females gathered at a mating centre, the more central males usually initiated most of the encounters with their more peripheral neighbours. The more central males also terminated most of their facing-past encounters, probably as a result of their tendencies to resume strutting nearer the females at the mating centre. When a territorial male disappeared, the vacancy was allocated to a more peripheral neighbour, one farther from the mating centre than the original occupant, without a noticeably increased frequency or intensity of antagonism.

First-year males lag behind older males in the growth of their gonads (Eng 1963). Some yearlings eventually established territories around the edge of a lek about half-way through the mating period, but yearling males were never seen copulating.

Section X. The combination of three processes can explain how a male acquires a territory at a mating centre: (a) the establishment of yearling males on territories around the periphery of a lek; (b) the centripetal movement of territorial males toward the mating centre as vacancies arise; and (c) the tendency for individual males to occupy positions in subsequent years at least as close to the mating centre as previously. The present study has provided evidence for the first two processes. Dalke et al. (1963) obtained some evidence that males usually return to the same lek and often to the same position in successive years. The hypothesis implies that a male's chances for success in mating would increase with increasing age.

Section XI. To clarify the behavioural manifestations of territoriality in sage grouse, a distinction is made between the territorial resident's aggression gradient and his isolation gradient. Male sage grouse occupy largely exclusive territories. Their ability to dominate agonistic encounters declines steeply across a narrow boundary zone. However, these isolation and aggression gradients are not congruent. The shapes of both gradients depend on the interactions of the resident and his neighbours.

Increased external pressure, owing to the attraction of males toward a mating centre, in conjunction with reduced internal resistance, owing to the central males' briefer facing-past encounters, could explain the generally smaller sizes of territories near a mating centre.

The males' interactions, which include both reciprocal and polarized components, suggest polarized territoriality, a form of social organization that merges features from the classical paradigms of both territoriality and dominance hierarchies. Polarized territoriality generates the radially differentiated social structure on a lek.

Section XII. A review of lek behaviour among grouse reveals only quantitative differences among the five species for which information on social organization is available. The lek behaviour of sage grouse represents the extreme development of this behaviour among grouse.

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APPENDIX

My discussion retains van den Assem's (1967) term gradient in its common meaning to designate a monotonic function in space. In mathematical terminology, however, field is the appropriate term for a function of spatial coordinates. If $a = F(x, y)$ is such a function, then the partial derivatives of the function ($\delta F/\delta x$, $\delta F/\delta y$), correctly specify its gradient.

A convex gradient is one that becomes distinctly steeper at some distance from the centre of the territory. Such gradients might in fact have sigmoid shapes, as I have suggested in Fig. 21. I distinguish between aggression gradients that have some pronounced convexity with respect to the centre of the territory, regardless of the probable presence of a point of inflection, and aggression gradients that lack any convexity.

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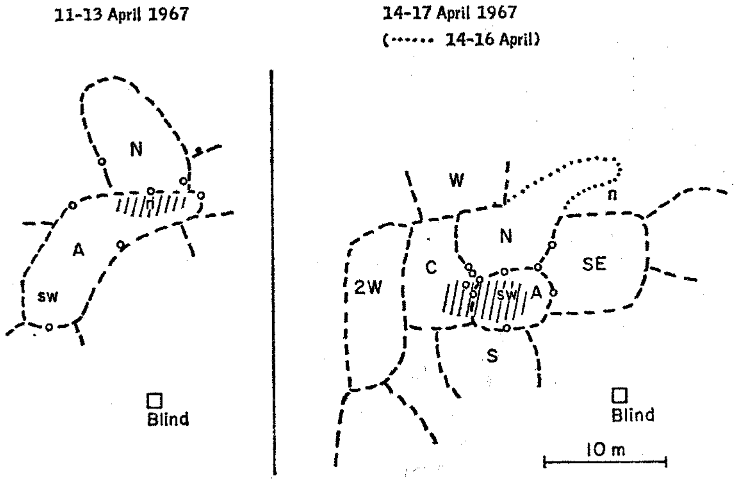
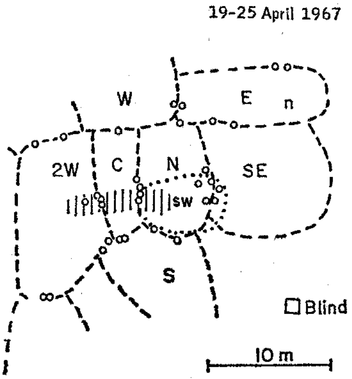
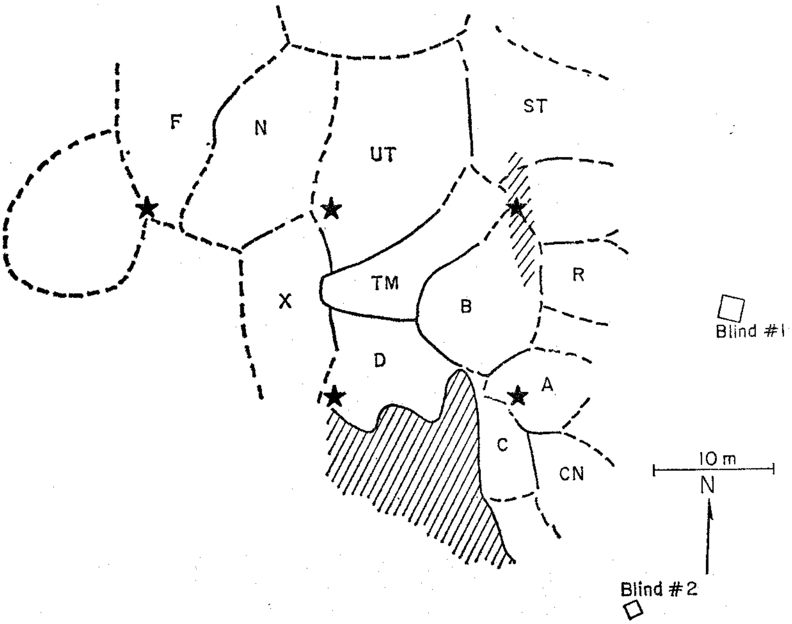
MAPS



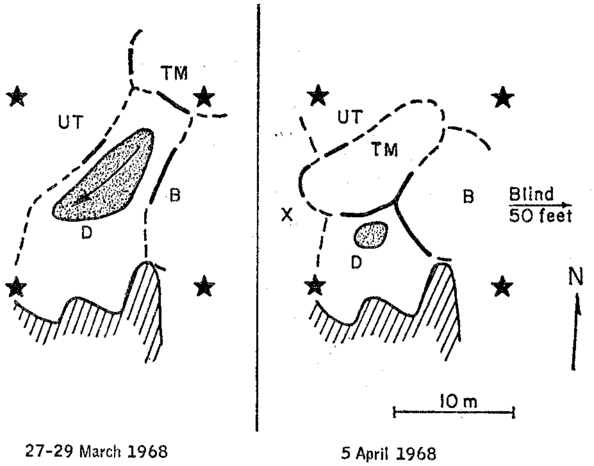
Map 1. East Mating Centre, Muddy Springs Lek, 1967. The mating centre (cross-hatching) shifted from the northern site (n) to the south-western site (sw). Interrupted lines indicate the approximate boundaries of males' territories; capital letters within each territory specify the individual males; locations of facing-past encounters appear as small circles.



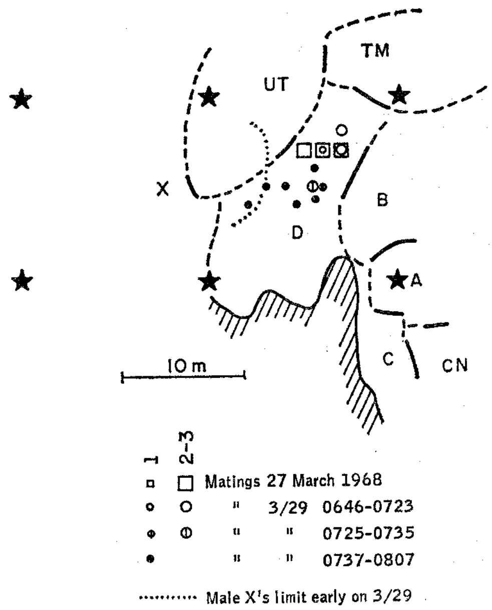
Map 2. Territories in 1967 after the disappearance of Male A. Male N occupied the area vacated by A (dotted line). Other symbols as in Map 1.



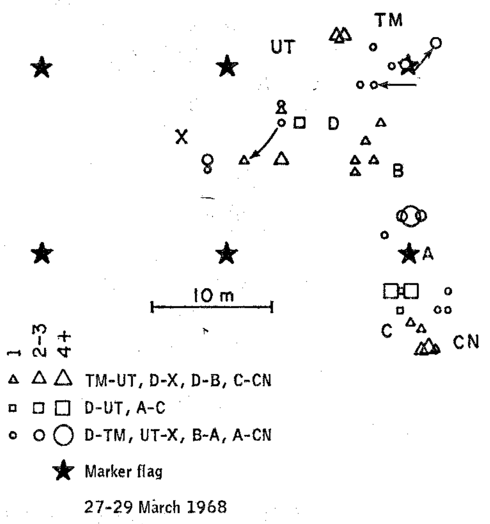
Map 3. Territories of individually identified males at least 2 years old (capital letters), 3 to 5 April 1968, Fords Creek Lek. Boundaries based on records of facing-past encounters appear as solid lines. Interrupted lines indicate less accurately known boundaries based on the males' movements. In reality facing-past encounters cluster in zones 1 to 3 m wide (see Maps 8b and 9b). Stars indicate positions of marker flags on a 15·4-m grid. Hatched areas are shallow depressions in the ground seldom used by displaying males. Several other males occupied positions south and west of the area mapped.



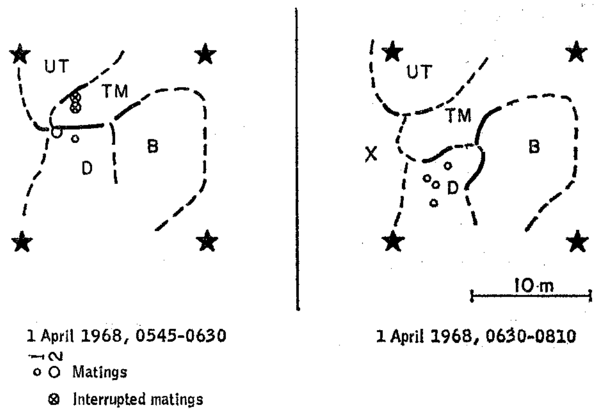
Map 4. The mating centre in 1968 gradually moved 8 m south-west. On 27–29 March the area used for mating (stippled) shifted but the boundary between males D and TM did not. On 31 March and 1 April both the mating centre and male D's boundaries moved (see Maps 6a and 6b). Finally, on 5 April, the mating centre and male D's boundaries were stable in their new positions. Other symbols as in Map 3.



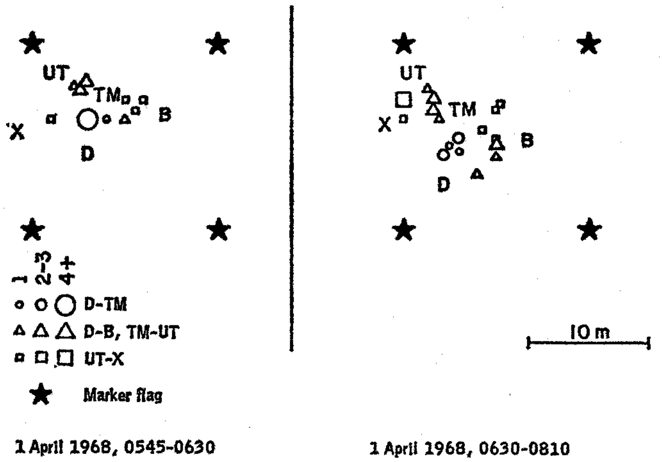
Map 5a. Territorial boundaries and matings, 27–29 March 1968. On the 29th male D's matings shifted southwest during the morning. Larger symbols indicate two or three matings at the same place. Territorial boundaries indicated by solid lines are based on facing-past encounters in Map 5b. Boundaries estimated from the males' movements appear as interrupted lines. Hatched areas are shallow depressions rarely used by territorial males. Stars indicate the positions of marker flags.



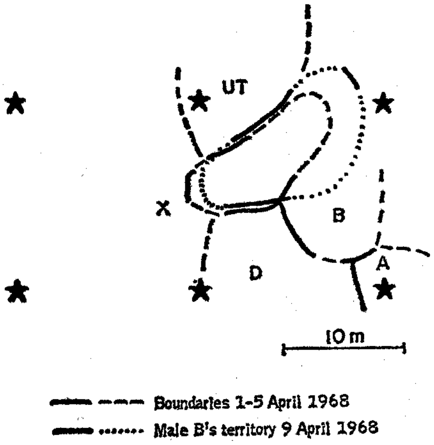
Map 5b. Facing-past encounters, 27 to 29 March 1968. Capital letters identifying each male are placed near the centres of their territories. Encounters between each pair of males are assigned one of three symbols. Larger symbols indicate more than one encounter at the same place. Occasionally an encounter moved more than a metre as one opponent retreated (arrows). Stars indicate the positions of marker flags. Map 5a shows territorial boundaries based on these facing-past encounters.



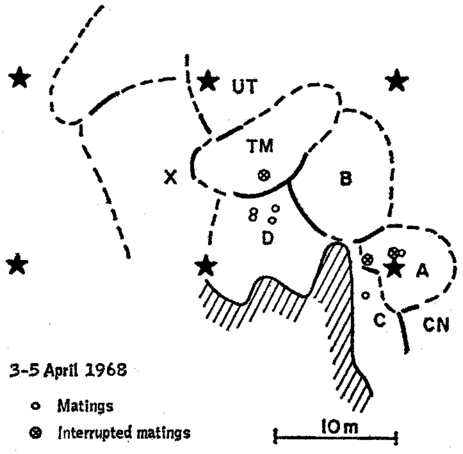
Map 6a. Territorial boundaries during the morning of 1 April 1968. The pack of females moved south in male D's territory (compare the positions of his matings earlier and later in the morning). See Map 5a for explanations of symbols. Territorial boundaries indicated by solid lines are based on facing-past encounters in Map 6b.



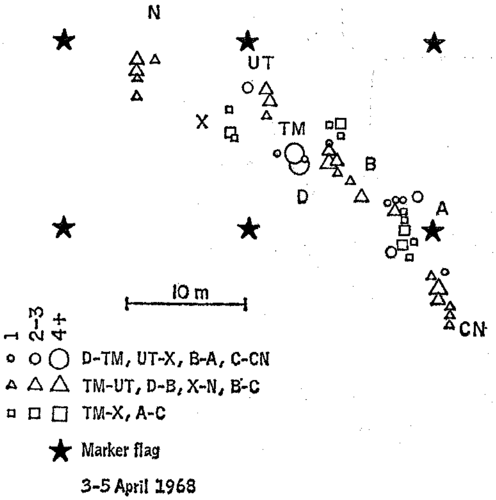
Map 6b. Facing-past encounters, 1 April 1968. See Map 5b for explanations of symbols.



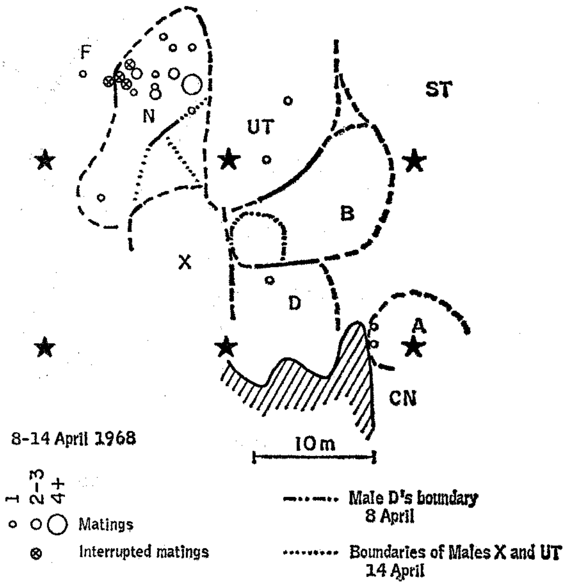
Map 7. Reoccupation of the territory vacated by male TM. Male TM disappeared after 5 April 1968, and by 9 April male B had reoccupied the vacated area with its original boundaries.



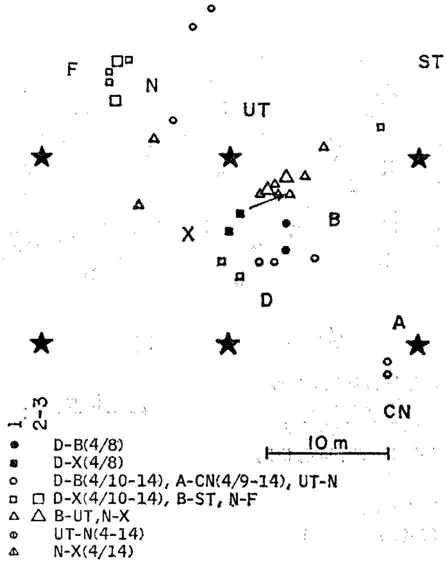
Map 8a. Territorial boundaries and matings, 3 to 5 April 1968. Boundaries indicated by solid lines are based on Facing-past encounters in Map 8b. See Map 5a for explanations of symbols.



Map 8b. Facing-past encounters, 3 to 5 April 1968. See Map 5b for explanations of symbols.



Map 9a. Territorial boundaries and matings, 8 to 14 April 1968. Boundaries indicated by solid lines are based on facing-past encounters in Map 8b. The mating centre has now moved to male N's territory, Males X and UT extended their boundaries into male N's territory on 14 April while male N was mating frequently. Male TM (Map 8a) has disappeared, and male B has occupied the vacancy, although for 1 day male D defended the western portion of TM's former territory. See Map 5a for explanations of other symbols.



Map 9b. Facing-past encounters, 8 to 14 April 1968. See Map 5b for explanations of symbols.

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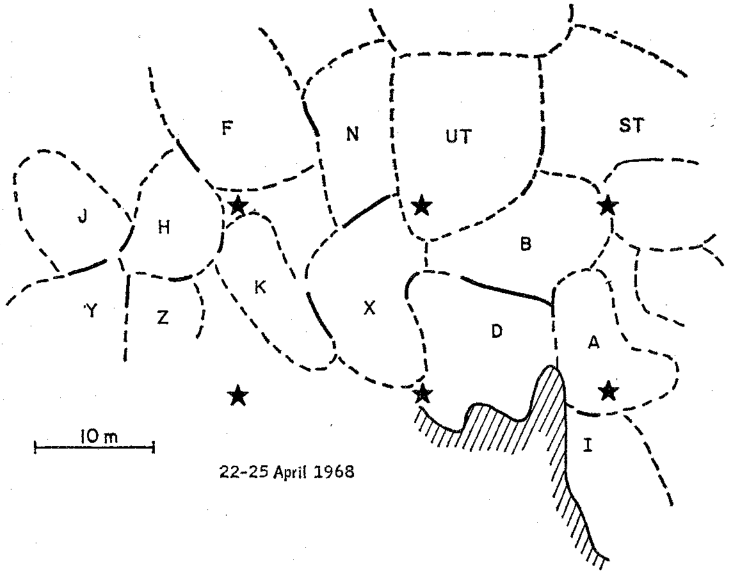
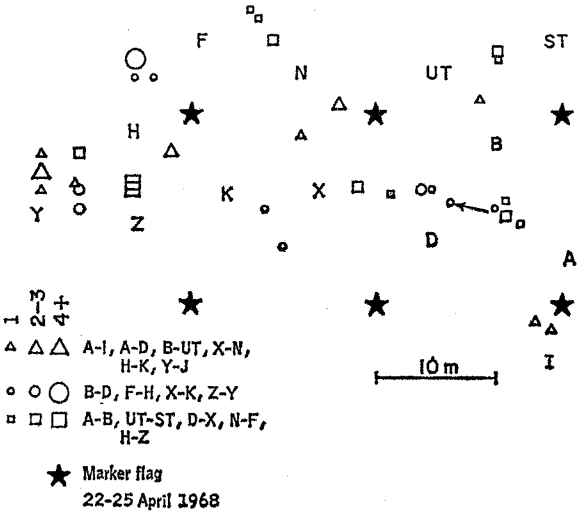
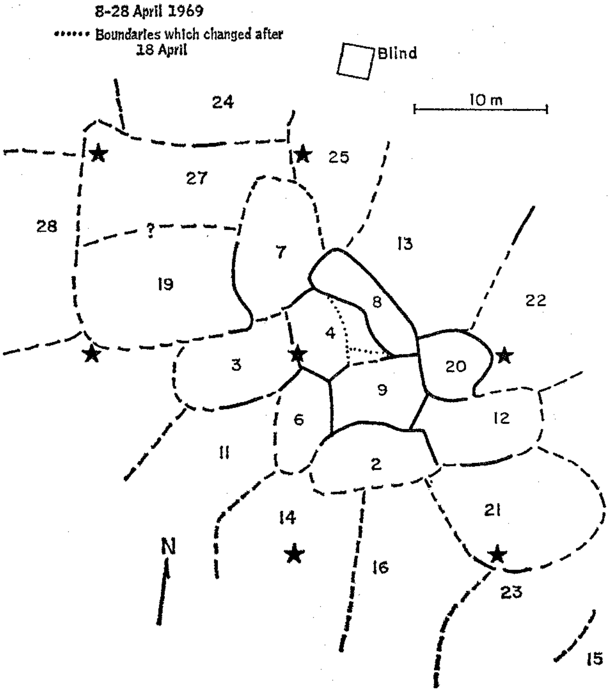


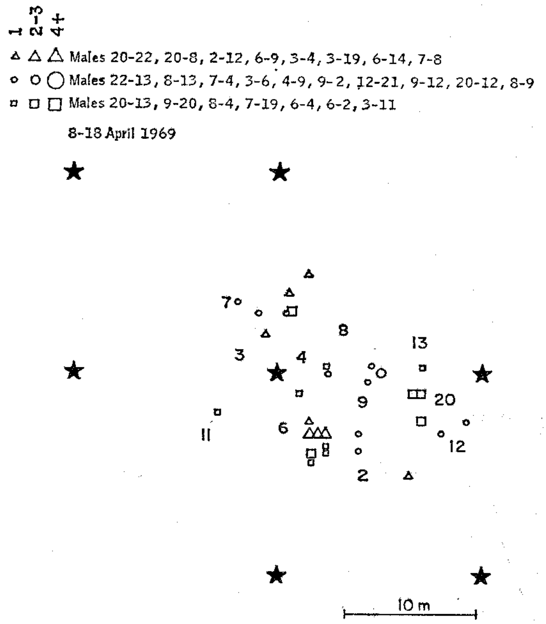
Map 10a. Territorial boundaries, 22 to 25 April 1968. Five yearlings (males I, J, Y, Z and K) occupied stable territories. Boundaries indicated by solid lines are based on facing-past encounters in Map 10b. See Map 5a for explanations of other symbols.



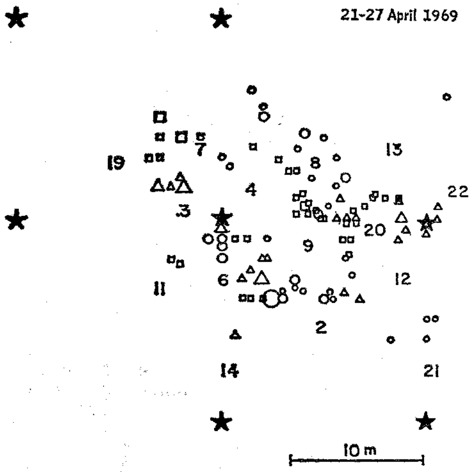
Map 10b. Facing-past encounters, 22 to 25 April 1968. See Map 5b for explanations of symbols.



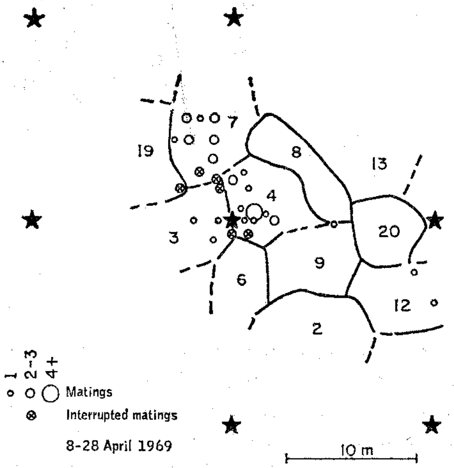
Map 11a. Territories of individually recognized males (numbers), 8 to 28 April 1969, Dry Sandy Lek. Boundaries based on records of facing-past encounters (see Map 11b and c) appear as solid lines. Interrupted lines indicate less accurately known boundaries based on the males' movements. Some boundary zones are actually far from one-dimensional, for instance between males 8 and 13, and between males 20 and 22. Stars indicate the positions of marker flags in a 15·4-m grid. Many other males occupied positions in all directions from the mapped area. Males 24, 25, 27 and 28 were yearlings.



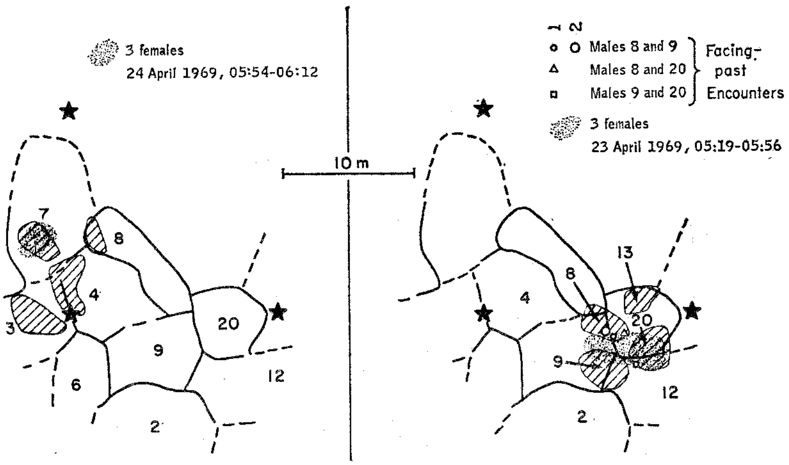
Map 11b. Facing-past encounters, 8 to 18 April 1969. Numbers identifying each male are placed near the centres of their territories. Encounters between each pair of males are assigned one of three symbols. Larger symbols indicate more than one encounter at the same place. Stars indicate the positions of marker flags in a 15·4-m grid.



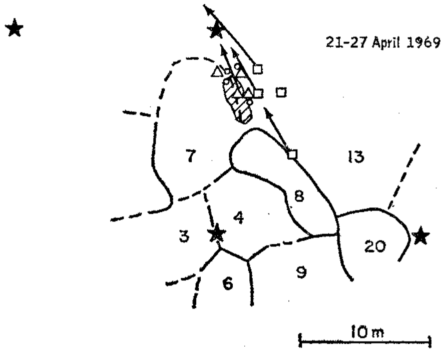
Map 11c. Facing-past encounters, 21 to 27 April 1969. Symbols as in Map 11b.



Map 12. Territorial boundaries and matings, 8 to 28 April 1969. Interrupted matings (⊗) occur near or within zones of facing-past encounters. Territorial boundaries represented by solid lines are based on facing-past encounters in Maps 11b and 11c.



Map 13. Males strutting in positions (hatched) along the boundaries of their territories nearest a group of females (stippled area). Male 8 strutted at one end of his territory or the other depending on where females were closest. Males sometimes encroach into a neighbour's territory to strut nearer the females. On 23 April males 8, 13 and 9 strutted unusually far beyond their regular boundaries and even met their neighbours in facing-past encounters beyond the usual zone. It was unusual for females to remain in the territory of male 20, but they often stayed in the territories of males 4 and 7.



Map 14. A yearling male (25) chased persistently by his older neighbours. Male 25 preferred to strut in the hatched area but was frequently chased away by males 7 (triangles), 8 (circles) and 13 (squares). Arrows indicate chases. Symbols without arrows are facing-past encounters. See Map 11a for further explanation.