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TERRITORIALITY AND NON-RANDOM MATING IN
SAGE GROUSE CENTROCERCUS UROPHASIANUS

A thesis submitted to the Faculty of The Rockefeller University
in partial fulfillment of the requirements
for the degree of Doctor of Philosophy

by
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Approved for publication.

June, 1970

The Rockefeller University

New York, New York

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PREFACE

During my three seasons in the field my work was aided by the cooperation and solid advice of four biologists in Wyoming and Montana: Dr. Kenneth Diem, University of Wyoming, Laramie; Duane Pyrah and Neil Martin, Montana Department of Fish and Game, Lewistown; and James June, Wyoming Game and Fish Commission, Green River. Without their help and hospitality my work could not have been done. In 1968 the Montana Fish and Game Department allowed me to live in their house-trailer in Winnett. V.N. Bell, Bosler, Wyoming; W.H. Bell, Grass Range, Montana; and the Bureau of Land Management, Rock Springs District Office, Wyoming granted me permission to work on land which they owned or administered. Karen P. Wiley helped with most of the field work in both 1968 and 1969.

Throughout my study I benefited from the guidance and friendship of many colleagues at The Rockefeller University in the laboratories of Drs. Peter Marler, Donald Griffin, and Theodosius Dobzhansky. Peter Marler especially encouraged me in confronting problems in the evolution of social systems and animal communication. His perceptive analyses, wide-ranging interests, and acceptance of me as a colleague stimulated much of my progress during my years at The Rockefeller University. For discussions of the genetic implications of mating systems I relied heavily on discussions with Dr. Dobzhansky and his colleagues Francisco Ayala, Lee Ehrman, and Rollin Richmond. Much essential assistance, including help with many details of organizing field trips, came from Kathryn Harpham, Cate Dolan, and Ann Lutjen of Dr. Marler's laboratory.

usually recur from year to year at the same places within a lek, a male becomes successful in mating by acquiring a territory at a mating center.

The behavior of males near a mating center 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. However, these differences apparently depended on the proximity of the males to females rather than on intrinsic differences among the individual males. Most males two or more years old, whether near a mating center or not, responded similarly to the presence of females within their territories. The Strut display shows extreme species-specific stereotypy in its internal timing. Although individual differences in the Strut display were detected, these differences were slight and did not correlate with the males' successes in mating.

Since the mating centers tend to remain in the same place from year to year as well as from day to day, females do not have to discriminate among individual males in order to identify a mating center. Females might learn the location of a mating center. Naive females could locate a mating center by observing other females congregated there or by following experienced females. Only limited guidance could come from the generally smaller territories of males near a mating center.

The males' interactions specify how a male eventually occupies a territory at a mating center. These interactions merge features of two classical paradigms for social interaction: the territory and the dominance hierarchy. Reciprocal interactions among males included the limited scope of neighbors' intrusions into each other's territories and neighbors' encounters as equals in boundary zones between their territories. Non-reciprocal, or polarized interactions, among males resulted from the attraction of males toward a mating center. Since their more peripheral neighbors tended to encroach beyond their boundary zones toward the females gathered at a mating center, the

To explain the evolution of lek mating systems, at least among grouse, one must address three problems: (1) a male life cycle with delayed onset of reproduction; (2) the absence of male parental care; and (3) the aggregation of displaying males.

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Figure 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.

In several other lek-forming species of grouse, the males' interactions show clear resemblances to classical territoriality: Black Grouse Lyrurus tetrix (especially Kruijt and Hogan, 1967; and Koivisto, 1965); Sharp-tailed Grouse Pedioecetes phasianellus (Lumsden, 1965); and Prairie Chickens Tympanuchus cupido (Hamerstrom and Hamerstrom, 1960). Male Black Grouse occupy small, but exclusive territories on a lek, and neighbors encounter each other along mutual boundaries. Yet in all these species successful matings are distributed non-randomly among the males (Chapter XIII, Section A).

It thus remains unclear whether ordinary conceptions of dominance hierarchies or territoriality apply to the social interactions of male grouse on their leks and explain the non-random distribution of matings among them. Kruijt and Hogan (1967) have begun quantitative observations on Black Grouse leks, but nothing similar has been attempted for Sage Grouse. Since Sage Grouse show an extreme form of a polygynous mating system, a better understanding of their behavioral 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. As a further basis for understanding territorial behavior, a distinction will be drawn between an aggression gradient and an exclusion gradient in the expression of territorial behavior. Finally, the body of this thesis will explore the behavior of male Sage Grouse on their leks in an attempt to recognize and quantify the interactions which might regulate the species' mating system. To pursue this goal, the bases of mate selection by females will also require consideration.

II. DOMINANCE HIERARCHIES AND TERRITORIALITY

Differences in social organization ultimately depend on differences in the patterns of interactions among individuals. Two classical paradigms for social organization, the dominance hierarchy and territoriality (see Allee, 1938; Collins, 1944; Howard, 1920; Nice, 1941), differ in the extent to which individuals' interactions are polarized. In a dominance hierarchy individuals are ranked by their access to some resource, such as food or reproductive partners, and often by their success in agonistic encounters. Hierarchical organization of individuals depends on two sorts of polarity in the social system: (1) individuals of different rank differ in their behavior; and (2) interactions among individuals of different rank lack reciprocity. To understand a hierarchical social organization one must identify and characterize the nature of the polarities in individuals' interactions. In contrast, territorial individuals interact reciprocally, at least in those species in which individuals usually restrict their activities to their own territories. Each individual inhabits his own territory, and neighbors meet as equals at their boundaries.

In many species, however, territorial individuals do not restrict their movements to their own territories. In these species a bird's territory emerges as the area in which it dominates all other conspecific individuals except perhaps its mate. At any time the territorial resident can chase away an intruding individual or supplant the intruder at a food source within the resident's territory. For example, the territory of a nesting pair of Bicolored Antbirds Gymnophis bicolor constitutes that area around their nest where the pair can supplant all other individuals from the choice feeding spots above swarms of army ants (Willis, 1967). In many species of birds individuals maintain territories during the breeding season but during the winter form flocks or range far beyond their former nesting territories. In a number of these species an individual's rank at a food source depends on the individual's distance from its previous nesting territory

Figure 2. Representative aggression gradients.

come from patterns in the reoccupation of vacated territories. Individuals should relinquish their original territorial positions in order to move into more desirable positions. In several species of birds when territorial individuals are removed or disappear naturally, the vacated areas are reoccupied by newcomers, although sometimes only partially (Bendell and Elliot, 1967; Watson, 1967; Orians, 1961; Delius, 1965; Stewart and Aldrich, 1951; Hensley and Cope, 1951; Holmes, 1966). Except in the study of Red Grouse Lagopus lagopus scoticus reported by Watson, in all these studies the previous status of the newcomers was unknown. Watson reported that most new occupants were birds previously without territories, although in some cases territorial individuals relinquished their original positions in order to establish new territories in the vacated areas. Clear evidence for ranking among territorial individuals according to their territorial locations is, therefore, not available for any species. Yet for many species certain habitats are more favorable for nesting and attract individuals establishing territories (for instance, Kluyver and Tinbergen, 1953). In several polygynous species which nest in marshes, differences in the vegetation in males' territories correlate with the number of mates the males can attract (Verner, 1964; Willson, 1966; Kluyver, 1955). In these species individual males might be expected to relinquish their original territorial positions when vacancies arise in order to move, perhaps in the following year, into more desirable positions.

This paper will suggest that polarized territoriality has an important role in regulating the mating system of Sage Grouse. Fully adult male Sage Grouse occupy nearly exclusive territories on their communal display grounds and have Type A aggressive gradients. However, since females congregate for mating at particular sites (mating centers) within a lek, the locations of territories differ in the opportunities they present for mating. Polarity in the territorial behavior of males involves (1) differences in the behavior of territorial males established at different distances from a mating center and (2) non-reciprocal interactions of territorial males. Males move their territories in

III. SKETCH OF A MORNING'S ACTIVITY ON A LEK

A brief synthesis of the activity on a Sage Grouse lek during a typical morning in the mating period will help in reading the detailed chapters to follow. Many of the points introduced here are based on my own observations or interpretations and will receive full treatment in later sections.

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 an hour before sunrise. The males occupy small, contiguous territories, 30-200 square meters in area. Each male occupies the same territory every day. Within his territory each male assumes the Strutting Posture (Figure 5), with his tail cocked and fanned, his head raised, and the white feathers and black plumes on the sides of his neck erected. Each performs repeatedly at intervals of 7-10 seconds an elaborate, stereotyped display, called a Strut. In this display, by a complex sequence of motions, a male inflates a large expansion of his esophagus (Figure 4) and then suddenly deflates it to produce a peculiar sound, coo-oo-pouink! In the breeding season the males' esophageal sac enlarges, and the skin of the chest overlying this sac becomes edematous and vascularized (Clarke, Rahn, and Martin, 1942). From time to time two males on neighboring 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 (Figure 8). In high-intensity encounters the males close until they are side-by-side a few inches apart facing opposite directions. An encounter usually involves some jockeying backwards and forwards for position. Either male may dart forward a few inches and force his opponent to retreat. However, their roles switch quickly, each male retreating in turn as his

extended. A female usually copulates only once each season and lays her entire clutch of 6-8 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 cooperation at all from a male.

TABLE 1

Two Bases for Classifying Avian Mating Systems

Association between mated pairs	Breeding sex ratio
I. Durable pair-bonds	A. Monogamy
II. Promiscuity	B. Polygamy
	B'. Polygyny
	B'', Polyandry

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 stiff feathers on the sides of his chest (Figure 4). 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 for 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 balloon and collapse, two sharp snaps are produced approximately one tenth of a second apart. A peculiar resonant quality accompanies the snaps, and several brief, soft coos precede them. Thus, the entire acoustic output from the display sounds roughly as follows: swish---swish---coo-oo-poink. Following a Strut the male returns to Strutting Posture. The display itself lasts slightly more than 2 seconds. A male usually Struts at intervals of 7-10 seconds; intervals of 5-6 seconds are rare. The sounds of the males Strutting on a lek can usually only be heard within several hundred yards of the lek. In contrast, the white feathers of the males' chests, which bob up and down during their displays, are conspicuous at great distances.

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 (Figure 5). 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.

Sleeked, Collapsed, and Semi-collapsed 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.

Figure 4. Strut. The chest sac is being lifted as the wings scrape the sides of the chest.

Figure 6. Semi-collapsed Posture.

Figure 8. Facing-past Encounter.

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 5-10 seconds 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 behavior apparently only follows completed copulations (Chapter VII, Section B). In other situations females occasionally shake themselves briefly, but after a completed copulation a female will continue Post-copulatory Ruffling for 10-15 seconds and even sporadically thereafter. As the Ruffling subsides, the female begins prolonged periods of preening, which often last fifteen minutes or more.

Quacking Call: a call uttered by flying females. The tonal quality suggests the quacking of a female Mallard. Unlike a duck, however, the Quacking Call of a female Sage Grouse is usually single, rather than rapidly repeated. 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.

V. STUDY SITES AND PROCEDURES

A. 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; $41^{\circ} 32' 30''$ N, $105^{\circ} 34' 40''$ W; R. 73 W, T. 18 N, section 9; elevation 7200 feet), the same lek Scott (1942) had observed in 1940 and 1941. Work continued from 10 April through 25 April. In 1968 I worked at the Fords Creek Lek, Fergus County, Montana (5 km north-north-west of Grass Range, Montana; $47^{\circ} 08' 15''$ N, $108^{\circ} 53' 05''$ W; R. 22 E, T. 16 N, section 24; elevation 3550 feet), the lek that Lumsden (1968) observed in 1965. Observations here continued from 16 March through 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; $42^{\circ} 13' 55''$ N, $109^{\circ} 14' 40''$ W; R. 104 W, T. 26 N, section 17; elevation 6810 feet). After observations began on 31 March, they continued through 28 April.

B. Observation Procedures

Each year on arrival I erected a blind with a clear view of one mating center. Subsequently, aside 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 yards 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.

Accurate counts of the numbers of females were even more difficult to obtain, owing to the large areas covered by the leks in 1967 and 1969 and to 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.

D. Recognition of Individuals and Age-classes

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

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 when he is 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 remained stable from day to day. By carefully recording the patterns of spots I could identify 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. Figure 9 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 center.

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-covert pattern changed by the deletion of several feathers. Although I did not see the fight which I presume was responsible for this 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 10 tail feathers on each side or 9. A few males had 9 on one side and 10 on the other. I had difficulty counting the tail feathers of males more than 30 meters from my blind. I recorded the numbers of rectrices of all closer males several times during the season.

Occasionally I could identify an individual male by other peculiarities. 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 which 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

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 center 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.

F. Records of Spatial Relationships

In order to facilitate locating birds on the lek, I placed small flags on a 50-foot (15.4-meter) 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 meter length of heavy wire. The birds appeared to ignore these markers. To aid further in locating positions on the lek I prepared base maps on which all salient clumps of sagebrush were indicated. I judged that inaccuracies in locating a bird's position were probably no more than one-half meter. However, birds over 50 meters 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 29 mornings in 1968 and 1969 I recorded birds' activities on time-lapse film during one to two and a half hours. The field of view usually included 5-10 territorial males at various distances from a mating center. In 1968 I used a filming speed of one frame every 3-4 seconds; in 1969 I filmed at about 1 frame/second. On each morning I determined the precise rate with a stopwatch. Since males Strutted every 6-10 seconds and remained in one position between Struts, except

of time-lapse film from 27, 29, and 31 March and 1 and 3 April 1968. All sequences were separated by at least five minutes. Each male in each six-minute period was classified according to his proximity to females. Three situations were recognized: (1) a female or females within his territory (Situation T); (2) a female or females within 10 meters of the male in a neighboring territory but not in his own territory (Situation N); and (3) no females within 10 meters (Situation O) during the six-minute period. Thus the behavior of individual males could be compared under conditions of roughly equivalent proximity to females. Eight males appeared in eight or more of the 28 six-minute samples: Male D in 28 samples; Male B in 27; Male X in 22; Males TM and UT in 19 each; Male A in 18; Male C in 10; and Male CN in 8 samples.

In each six-minute period I counted how many times each male in view during the entire period Strutted. In addition, in every third frame (about every 12 seconds) I recorded whether the male was in Strutting Posture, in Semi-collapsed Posture, in Collapsed Posture, in a Facing-past Encounter, mating, or chasing an intruding male (see Chapter IX, Section 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 six-minute 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 six-minute 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 seconds, varying slightly as my filming rate changed). These estimates are not reliable for very long and very short Facing-past Encounters. Brief encounters, which did not appear in a sampled frame (recall that I sampled every third frame) were

mating center or not. For each pausing female I recorded whether or not she was within 3 meters of a male, whether or not she was within 3 meters 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 20 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 20 females.

between rises in the surface of the land at least half a kilometer 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 half a meter above the ground, a broad valley may offer advantages in detecting approaching predators (see Chapter IX, Section I). The bird would have a clear view of the ground as far as the nearest rises in the prairie, often half a kilometer 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 explain entirely 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 centimeters 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 which did not form sod and which 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 thus occurred 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

of my blind (northern site; n, Map 1). However, that evening I watched Male A twice move about 10 meters south-west and begin to Strut in an area about 10 meters north-west of my blind (Map 1). He encountered a neighboring 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 meters to the north, but after about 15 minutes they dispersed and gathered again around Male A, 15 meters 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 meters north and others the area 10 meters 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 meters north of my blind, and as many as 42 congregated in the area 10 meters south-west instead. Male A never left this area all morning and copulated over 30 times. On subsequent mornings females always congregated at this same place and never again revealed any interest in the site north of my blind. This south-western site one 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 center in 1941 which 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 16 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 may have enhanced the instability of this lek. I began my observations on 16 March. Females never exceeded 10 nor showed any consistent localization until 27 March, when females congregated in the area used by Male D. I saw matings for the first time that season on 27 March. On 29 and 31 March large packs of females assembled in the same position, but before activity had ended each morning the

females had gradually drifted 8 meters south-west (Maps 4, 5ab). 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 centimeters 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 meters south-west of the area in which they had originally congregated. Through 5 April I had observed the lek from a blind placed 25 meters from the pack of females. On the afternoon of 5 April I erected a second blind (Blind #2, Map 3) on a platform 1.2 meters high in hopes of obtaining a better vantage for recording the birds' spatial relationships. The new blind was also 25 meters 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 meters north-west of Male D's territory and farther from both of my blinds (Map 9ab). Especially when the females returned after an eagle had flushed the grouse at 05:28, 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 may not have influenced the shorter and more gradual shift in the position of the mating center. Possibly mating centers are less well localized in small leks and may shift positions over distances of 8 meters or so. In 1969 on the large Dry Sandy Lek, three mating centers which I could clearly observe remained in the same positions throughout the season. In the mating center which I studied thoroughly that year virtually all matings occurred in an area 5 x 8 meters.

Figure 10. Four mating centers on the Dry Sandy Lek, 1969.

Forty to 100 males displayed around each mating center (hatched areas).

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 behavioral regulation of their mating system. After presenting evidence that frequent mating by a male depends on the coincidence of his territory with a mating center, subsequent sections will examine how such a coincidence might arise.

A. Stability of the Territorial Boundary

For many males the boundaries of their territories remained relatively constant over the three to four 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 center drifted 8 meters from its original location. In 1969, on the other hand, most of the fully adult males' territorial boundaries remained in essentially the same locations throughout the period from 8-28 April (Maps 11a, b, c).

B. Distribution of Matings Among Males

The territorial males varied greatly in their success in mating. Those established within or near a mating center accomplished virtually all the matings, while most males never mated during the entire season. Tables 2, 3 and 4 present data on all the copulations which 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 (see Chapter IV, Section B). Vigorous Post-copulatory Ruffling seemed specific to completed copulations. If a male mounted but did not lower his tail before a neighboring male interrupted the copulation, the female never showed such vigorous ruffling or persistent preening. A completed copulation presumably inseminated the female,

Table 3

Copulations Recorded on the Fords Creek Lek, 1968. For explanation see Table 2. Maximum number of males on this lek = 30.

Date	Individual Males								Unident. Periph.	B	C	Total Number of Completed Copulations
	D	N	UT	TM	F	A	X	ST				
27 March	7											7
28	2											2
29	14											14
31	6			1								7
1 April	7		(1)	(1)					1,1			9
3												1
4	3					1(1)						4
5	1			2(2)					1		(1)	4
8		4(1)		Absent								4
9		3(1)	2		2						Absent	7
10	1	4(3)			1(1)							6
12		4	1			2		1				8
14		10					1			(1)		11
15			1									1
22												0
23			1									1
24									1			1
25												0
Total Number of Completed Copulations	41	25	5	3	3	3	1	1	1,1,1,1	0	0	87(13)
%	47.2	28.8	5.8	3.5	3.5	3.5	1.2 x 6					

Table 4

Copulations Recorded on the Dry Sandy Lek, Mating Center #3, 1969.
For explanation see Table 3. Maximum number of males around this
mating center = 52.

Date	Individual Males								Total Number 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						9
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 Number 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	

* Matings with an abnormal female (see text); not included among
completed copulations.

problems, so I probably overlooked more matings than I did in previous years.

On four mornings in 1969 a female with peculiar behavior visited the lek. On each of these days 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. Males would repeatedly attempt to effect cloacal contact with this female and finally simply dismount. Furthermore, the female never performed Post-copulatory Ruffling. Her pre-copulatory behavior was also abnormal. 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. On 23 April the males' repeated treadings actually drew blood from the abnormal female's back, which stained the white chests of the males attempting to copulate with her. Since no more than one such female appeared on any day, and no other female in other years showed similar behavior, I assume that the same individual came all four 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 center. In each year two or three males, 5-10% of the males present around each mating center I studied, accomplished over 75% of all completed copulations there. Figure 11 shows how skewed the distribution of matings among the individual males in fact was. Data collected at each of the three mating centers I studied are superimposed. Males from each year are ranked on the abscissa in decreasing order of success in mating. Since the total number of males surrounding each mating center ranged from 30 to 60, 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.

Distribution of matings among males
at three mating centers

Figure 11. The distribution of matings among males at three mating centers. Individual males are listed on the abscissa in decreasing order of their successes in mating. The ordinate is the percentage of the total number of completed copulations observed each year.

In contrast, male Black Grouse remain within their territories even when females are on the lek. In the exclusiveness of their territories, male Sage Grouse seem to resemble Black Grouse more than Prairie Chickens (see below). The high frequency of interrupted copulations in Sage Grouse might instead stem from the small size of the males' territories, which had a minimum area of 30-50 square meters in contrast with 75-100 square meters in Prairie Chickens and Black Grouse (Chapter XIII, Section A). 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, I never felt that a female's chances for copulation were limited.

Do those males more successful in mating tend to interrupt the matings of their less successful neighbors more than vice versa? The small numbers of interrupted matings which I observed cannot provide a conclusive answer to this question (Tables 5, 6, and 7). In some cases, pairs of neighboring 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 sometimes fewer matings than his opponent (compare Males N and F, 1968, and Males A and C, 1967). Usually the males less successful in mating seem to have a greater proportion of their attempted matings interrupted, although these interruptions as usual involve matings attempted near territorial boundaries. If females congregate within one male's territory, then any matings attempted by neighboring males are most likely to occur near the territorial boundary.

Within his territory a copulating male appears immune from his neighbors' interruptions. Only matings attempted near or within the zones of Facing-past Encounters, which define territorial boundaries, risk interruptions by neighboring males. A male achieves success in mating by occupying a territory that includes a mating center or part of one, not by directly preventing matings by other males. By contrast,

Table 5

Interrupted Copulations, Muddy Springs Lek, 1967

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

Table 6

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

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

Thus, one sort of polarity is especially prominent among territorial male Sage Grouse surrounding a mating center: their differing successes in mating.

VIII. BASES FOR FEMALE SELECTION

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

A. Behavior of Females

Before discussing how females might select a place to mate, I shall describe in more detail the behavior 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 10-30. Often two or three males in Collapsed Posture accompany these flocks without performing any displays. These males probably are yearlings, as I shall discuss in a later section (Chapter IX, Section J). The loose groups of females wander across the lek without much localization of their movements. The females in these early groups show little behavior that suggests an inclination to mate. The females usually space themselves 1-3 meters 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.

In 1969 when I first arrived at the Dry Sandy Lek the females exhibited similar behavior. On 31 March and 1 April dispersed groups of females, usually spaced 1-3 meters apart, wandered irregularly around the lek. Often these groups included males in Collapsed Posture. The females spent much time preening and showed no pre-copulatory

Figure 12. Numbers of females during the morning of April 16, 1969.

Dots, number of females at mating centers; open circles, number of females not at a mating center; crosses, number of flying females.

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, they usually 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 a minute and then began to walk. Early in the morning the paths of walking females rarely showed signs of aimlessness. Instead, females usually walked steadily and directly toward the nearest mating center. 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 center. 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 ($\pm 30^\circ$) the nearest mating center. Before and around sunrise the majority of walking females were headed for the nearest mating center (Figure 13). When a female came within 15-20 meters of a pack of females congregated at a mating center, she rarely stopped or deviated before entering the pack.

On a large lek with several mating centers females did occasionally either walk or fly a short distance from the vicinity of one mating center to another mating center. In 1969 I observed such behavior 10 times between 9 and 18 April.

Once in a pack at a mating center, 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 motivated to copulate. In spite of the fact that the females were usually spaced within a half meter 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 one meter in radius around the front of the Strutting male. Since the male Strutted back and forth within the center 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 pre-copulatory Solicitation Posture, she would dash forward a meter or so and chase briefly any female in her path. In 1967 on several mornings I observed one female that exhibited unusually aggressive behavior toward the other females. This individual spent most of a morning dashing vigorously after other females, often over distances of 2-5 meters. 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 the same individual female with abnormal behavior appeared each of these mornings. Other observers have noted females which showed elements of male behavior (Scott, 1942; Patterson, 1952; Lumsden, 1968).

Females usually adopt the Solicitation Posture near the termination of the male's Strut. The male waits 7-10 seconds after his previous Strut before mounting. The female may relax before he mounts and then solicit again following his next Strut. Usually if a female continues to solicit she progressively increases the duration and intensity of her Solicitation Posture. Eventually a female may hold her Solicitation Posture continuously between successive Struts of the male. Ordinarily a female does not solicit except when she is within one-half meter of the front of the male, but intensely and persistently

soliciting females sometimes assume their posture more than a meter from the male. Usually the male will mount any female that will hold a Solicitation Posture while he steps toward her. Occasionally, though, especially later in a morning a female may Solicit repeatedly and intensely after 5 or more Struts before the male will mount. Thus continued interaction of a male and a female appears necessary to stimulate both sexes to copulate. Usually, though, a male will respond to any female that holds a Solicitation Posture. Once a male mounts copulation is usually completed in 3-5 seconds, unless a neighboring male interrupts the copulation.

Most females probably mate only once a season. By observing 16 marked females, Lumsden (1968) obtained evidence that each female visited a lek on several mornings before she was seen to mate. None of the seven females observed mating was ever seen again. Pyrah (1964) records a captive hen which laid six fertile eggs after she was removed from any contact with males. Her last fertile egg was laid at least 17 days after she could possibly have copulated. Thus one copulation may fertilize a female's entire clutch, which averages 6-8 eggs. On the other hand, the number of copulations which occur at a mating center probably exceeds the maximum number of males surrounding the mating center. At the mating centers which I 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 arise from an unequal sex ratio at that season, or from 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 the number of times a female mates in one season. Available evidence suggests that each female visits a lek on several

They usually flew over the lek, landed in the periphery, and then walked to the mating center. The relatively direct paths of females walking toward a mating center early in the morning suggests that many individual females know at least approximately where the mating center is located.

A female could use five classes of cues in order to locate a mating center: (1) individual differences among the males which correlate with their success in mating; (2) overall patterns in the distribution or activity of males within a lek; (3) the presence of a conspicuous pack of females at a mating center; (4) guidance from other females which had visited the mating center previously; and (5) memory of the topography of the lek after her first few visits.

B. Individual Differences Among Males

Evidence presented in Chapter VI suggests that mating centers recur from year to year at roughly or precisely the same sites within a lek. Thus the mating centers within a lek apparently show a constancy of location comparable to the traditional locations of the leks themselves. This stability in the locations of mating centers 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 25-50% (Chapter 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. Table 8 presents counts of the numbers of frames between two distinctive stages in the Struts of different males in 1967. Frames were counted between the time at which the male's chest sac reached its highest position during its first rising phase and the

Table 8

Durations of Strut Displays by Different Males in 1967.

Figures are numbers of frames between two distinctive stages in the Strut (see text).

Frames/ sec(1)		Males, ranked in decreasing order of success in mating							
		A	C	2W	N	6W	S	SE	W
		1 ⁽²⁾	2	3	4	5	7	7	7
24	N	-	3	-	3	-	7	-	-
	$\bar{X}$		44.3		42.3		45.14		
	SD		0.58		1.53		1.34		
	SE		0.33		0.88		0.51		
	CV ⁽³⁾						3.0		
18	N	12	3	-	14	-	4	5	-
	$\bar{X}$	30.0	31.7		28.8		31.0	31.4	
	SD	1.13	0.58		0.80		0.82	1.14	
	SE	0.33	0.33		0.21		0.41	0.51	
	CV	3.8			2.8		2.6	3.6	
12	N	18	8	14	27	10	-	-	9
	$\bar{X}$	20.9	20.4	20.9	19.6	19.9			20.0
	SD	0.94	1.06	0.92	0.89	0.57			0.87
	SE	0.22	0.37	0.24	0.17	0.18			0.29
	CV	4.5	5.2	4.4	4.5	2.8			4.3

(1) Approximate, since the camera settings were not calibrated. The figures in the table suggest that the filming rate at a camera setting of 24 was slightly greater than twice the rate at a setting of 12.

(2) Rank in mating success.

(3) Coefficient of variation: $100 \times SD/\bar{X}$

Figure 14. 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 meters in a neighboring territory (stippled histograms, N); and no females nearby (open histograms, O). The ordinate is Struts per six-minute period. In the histograms each small square represents data from one six-minute period.

that this category was heterogeneous⁶. Either males responded to females in neighboring territories with considerable variability, or I failed to isolate the cues to which the males responded. By comparing the black histograms (Situation T) for the males sampled, I could establish only one 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 neighbor, Male B, who never mated successfully (Wilcoxon matched-pairs ranked-sign test, $T = 2.5$, $N = 10$, $p < .01$; 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 neighbor, Male TM, often Strutted less frequently per minute in Strutting Posture (Table 9). 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 which mated frequently.

The sample in which Male D Strutted least frequently with females in his territory, 21 Struts/6 minutes, came nearly two hours 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 (Figure 15). Males with females in their territories Strut at high rates regardless of the time of morning.

Therefore, rates of Strutting correlate best with a male's proximity to females, rather than with the male's position on the lek or with the time of morning. Figure 16, based on the same data, emphasizes that males Strut at high rates more often when females are in their territories. Males at or near a mating center must Strut many more times in a morning than do more peripheral males. Their greater

Figure 15. 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 meters in a neighboring territory. Open circles: males with no females nearby. Data from 27 March - 1 April 1968. Larger symbols indicate more than one male with that value. Arrows indicate extreme values for Male D in Situation T.

Figure 16. Rates of Strutting in relation to proximity to females.

Table 10

Relationship between the durations of males' Facing-past Encounters and proximity to females. Figures in the table are numbers of encounters. Data from 28 six-minute samples, 27 March - 3 April, 1968.

Proximities of opponents to females	Durations of Facing-past Encounters						Total Number of Encounters	Number of Encounters with Wing-fights
	1-35 sec	36-60 sec	1.0-1.9 min	2.0-3.9 min	4.0-5.9 min	6.0+ min		
T-T ⁽¹⁾	14 ^{ab(2)}	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-D		1		1		1	3	0

- (1) "T-T" signifies that both opponents had females within their territories (Situation T). A male in Situation N has a female within 10 meters in a neighboring territory. A male in Situation O has no female nearby.
- (2) Comparisons: a, χ^2_1 (Yates correction) = 22.96, $p < .001$; b, χ^2_1 (Yates correction) = 11.82, $p < .001$; c, χ^2_1 (Yates correction) = 0.029, $p > .80$.

Table 11

Durations and frequencies of Facing-past Encounters by individual males at different distances from females.

Proximity to females	Male	Durations of Encounters						Number of Encounters			No. of Samples
		1-35 sec	36-60 sec	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

Frequencies of Facing-past Encounters might also differ among individual males. Comparisons among the males are complicated by two considerations: (1) each encounter involves the interaction of two individuals, so a male's behavior is influenced both by his own tendencies and by his neighbor's; and (2) different males have different numbers of neighbors. In order to minimize the effects of these complications, I determined the frequencies of Facing-past Encounters for pairs of males when each male's proximity to females was known (Table 12). 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 must 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/6 minutes) and O-O (0.24 initiations/6 minutes) and least frequent in Situation T-N (0.04 initiations/6 minutes). Between Male D and his neighbors B and TM, encounters are most frequent in Situation T-T (0.47 initiations/6 minutes), of intermediate frequency in Situation T-N (0.31 initiations/6 minutes), and least frequent in Situation O-O (0.09 initiations/6 minutes) (Table 12). Thus, the most successful breeder (Male D) encountered his neighbors, 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 too few for such definite conclusions. Encounters were always most frequent when two neighbors both had females within their territories. Since in these cases the females usually occurred near the two neighbors' 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 13 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 - 4 April, except 3 April). Encounters that occurred earlier than an hour after

Table 13

Proportion of Facing-past Encounters which Included
Wing-fighting. 27 March - 1 April, 1968

Opponents	Earlier than one hour after sunrise		Later than one hour after sunrise	
	Total Number of Encounters	Proportion with Wing-fighting	Total Number of Encounters	Proportion with Wing-fighting
D-TM	34	.21	13	.15
D-B	15	.20	3	0
D-X	5	.20	3	.33
Subtotals	54	.204	19	.158
TM-UT	11	.27	10	.10
B-A	6	0	5	.20
Subtotals	17	.176	15	.133
A-C	7	.57	9	.11
C-CN	17	.06	6	0
Subtotals	24	.209	15	.071
Grand Totals	95	.200	49	.140

Difference between earlier and later in the grand totals is just significant at .05 level: $\chi^2_1 = 3.95$, $.02 < p < .05$. No other comparisons show significant differences.

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 center in the territory of Male D. In all three categories Wing-fighting occurred in approximately one-fifth (0.18-0.21) of the earlier Facing-past Encounters. Later in the morning the frequency of Wing-fighting declined in all three groups, and the difference is significant in a X^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' behavior relate primarily to differences in their proximities to females.

In conclusion, these studies of territorial male Sage Grouse at least two-years old have revealed no clear differences in their behavior patterns or responsiveness to females which might explain the large differences in their mating success. Those individual differences which I did detect among males, for instance, the durations of their Struts, do not correlate with their differences in mating success. If the females use individual differences in the behavior of males to select a place to mate, they must depend on subtle distinctions. The obvious differences between males successful in mating and those unsuccessful stem from the presence of females at the mating center. For instance, the males' behavior 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.

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

E. Other Females

Does any evidence suggest that females use cues from other females when they locate a mating center? I attempted to determine in two ways whether pausing females were attracted to other females. Data from my samples of female activity in 1969 suggest that females pausing away from a mating center are associated with other females significantly more often than are walking females ($N = 500$, $\chi^2 = 14.11$, 1 df, $p < .001$). Also females paused within 10 feet of a male are near other females significantly more often than are females paused farther from males ($N = 267$, $\chi^2 = 5.37$, 1 df, $p < .05$). Yet females pausing farther than 10 feet from males associate with other females no more often than do walking females ($N = 360$, $\chi^2 = 2.88$, 1 df, $p < .05$). Therefore, females pausing away from the mating center are attracted either to a Strutting male or to the combination of a paused female and a Strutting male.

On 17 April 1969 I attempted to use a cluster of taxidermic models of females to decoy females approaching a mating center. I placed an artificial pack of five taxidermic mounts of females 45 feet from the mating center. The decoy failed to attract any live females, although a number walked directly past on their way to the mating center. The negative result is inconclusive since most of the females this late in the season had probably already visited the mating center at least once on a previous morning. So no direct evidence can confirm that individual females interact in locating the mating center. However, this possibility seems so likely that further experiments would be worthwhile.

Possibly a female first identifies the position of a mating center by seeing the conspicuous pack of females there. Since 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 centers. This hypothesis would require that females on their first visit arrive later in the morning than do females that have been there before. After visiting a mating center several times in one season, a female 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 center 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: 836) also suggest that yearling females breed later than older females. The behavior of yearling and older females requires further study.

If some females use cues from other females to locate a mating center, then females must eventually come to remember the position of a mating center after they have visited it several times in one season. In other words, some females must eventually recognize the position of the mating center independently of stimuli from other females.

F. Summary

A female probably uses a number of different cues to find the mating center and possibly different ones on her first visit as a yearling than on later visits. Since the mating centers 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. Much of the variability in the behavior of different males on a lek depends on their different proximities to females rather than on inherent differences between 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 centers. However, the density of male territories would provide some orientation for an arriving female. Further cues might come from other females which remember the position of a mating center from previous visits.

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 meters beyond their usual zones of Facing-past Encounters.

Strutting males only occasionally transgressed their boundaries and very rarely more than Male 8 did on this occasion. Males at least two years old avoided deep intrusions into each others' territories. Exceptions occurred occasionally when males were walking to their positions on arrival at the lek (this Chapter, Section 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 (this Chapter, Section G). In the former case, when males which had to cross an occupied territory in order to reach their own, they always adopted a Collapsed 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 neighbors. 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 (see Chapter VI). On this morning his neighbors X and UT transgressed their usual boundaries and encountered Male N 5 meters beyond their usual zones of Facing-past Encounters (Maps 9ab). Usually, however, a Strutting male, after encroaching slightly into a neighboring territory, retreated to his usual zone of Facing-past Encounters when challenged.

An inhibition against intruding into neighboring territories became especially evident in two situations. When Male A disappeared in 1967 and left a vacancy which included part of a mating center, the vacancy was only gradually reoccupied over a period of several days (this Chapter, Section H). Secondly, males did not intrude deeply into neighbors' territories to interrupt copulations (Chapter VII, Section 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, 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 3-4 weeks. However, other males' boundaries which 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 neighbors in the same zones over several weeks, although conspicuous features of the surface do not seem necessary for this stability of territorial boundaries.

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 11abc). The area in which he Strutted was long and narrow, 2.5 x 10 meters. 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

The shapes of the zones of Facing-past Encounters between pairs of neighboring 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 8ab, 9ab). Thus, pairs of males showed little evidence of selecting conventional sites at which to encounter each other.

C. Initiation of Facing-past Encounters

The initiations of Facing-past Encounters offer striking evidence of non-reciprocal interactions between territorial males. This polarity results from the attractiveness of the mating center for territorial males.

When females are present at the mating center, each male tends to Strut along the side of his territory nearest the mating center. Periodically his more central neighbor 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 neighbor to initiate a Facing-past Encounter. Consequently, of two neighbors the more peripheral one tends 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. A mutual initiation implies that 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. Usually one male dashed toward his opponent, who was Strutting or, occasionally later in the morning, sitting in Semi-Collapsed 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 neighbors. Occasionally a male would walk to his boundary even though his neighbor was not near the boundary. Often the neighbor would then walk to join the first male in an encounter. For each pair of neighbors in Figures 17 and 18 the more central one is starred, 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 center 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 center and yet must maintain his farther boundary against gradual encroachments by his more peripheral neighbors.

Patterns in the initiations of Facing-past Encounters between certain pairs of males tended to equalize later in the morning when females were absent or fewer. Table 14 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 neighbor, 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 neighbors, by the

INITIATIONS OF ENCOUNTERS BETWEEN NEIGHBORING MALES 1969

Figure 18. Initiations of Facing-past Encounters between neighboring males in 1969. For explanation see Figure 17.

Table 14

Initiations of Facing-past Encounters Earlier and Later in
the Morning, 27 March - 14 April 1968 (except 3 April)

How Encounters Initiated Between Neighboring Males	Time		χ^2_1 (Yates correction)	P
	Earlier than One Hour After Sunrise	Later than One Hour After Sunrise		
1 D $\rightarrow$ B B $\rightarrow$ D ⁽¹⁾	14 0	2 3	5.97	< .02
2 TM $\rightarrow$ UT UT $\rightarrow$ TM	5 4	12 0	4.02	< .05
3 D $\rightarrow$ TM TM $\rightarrow$ D	27 4	4 4	3.33	> .05
4 B $\rightarrow$ A A $\rightarrow$ B	5 1	4 1	0.41	"
5 A $\rightarrow$ C C $\rightarrow$ A	3 0	2 3	0.89	"
6 C $\rightarrow$ CN CN $\rightarrow$ C	16 0	4 1	0.40	"
3-6 Combined	51 5	14 9	8.23	< .01

(1) Data for the interaction of Males B and D pertain to the period
before Male TM's disappearance on 8 April.

male tended to terminate even those encounters initiated by his more peripheral neighbor. Table 15 includes the data from encounters between Males D and TM in 1968 and encounters between Male 9 and his more peripheral neighbors in 1969. In both cases the more central male, Male D or Male 9, terminated significantly more of the encounters initiated by peripheral neighbors than expected. At least in these two cases the more central male tended to terminate 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 (Chapter VIII, Section B).

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

Owing to their briefer Facing-past Encounters, males with females in their territories devoted much less time to Facing-past Encounters than did males with no females nearby (Table 16). Males with females in their territories spent 92% of their time in Strutting Posture and only 5% in Facing-past Encounters. In comparison, when no females were within 10 meters, males spent only 26% of their time in Strutting Posture and 38% in Facing-past Encounters. Other activities of males near females included chasing intruders (this Chapter, Section J) and mating. Males farther from females also chased intruders, although this activity never accounted for more than 2% 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-Collapsed or Collapsed 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 (Figure 19). Male D and other males established near the mating center, therefore, spent far more time

Table 15

Terminations of Facing-past Encounters Between Neighboring Males. In each of the three 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 neighbors.

				χ^2_1 (Yates correction) ⁽¹⁾	P
	D	TM	m		
D	29	1	0		
TM	3	3	1	6.81	<.01
m	4	3	1		
	More Central	More Periph.	m		
More Central ⁽²⁾	41	3	4		
More Periph.	5	7	3	8.36	<.01
m	20	10	0		
	♂ 9	Periph. Neighbor	m		
♂ 9	24	3	5		
Periph. Neighbor ⁽³⁾	3	0	0	6.72	<.01
m	3	1	0		

(1) H_0 = the more central neighbor (C) terminates encounters begun by the more peripheral neighbor (P) in the same proportion that P terminates encounters begun by C.

(2) This table includes all encounters between Males TM and UT, A and C, B and A, D and B, D and X, 1968.

(3) Includes Males 2, 6, 8, and 20 in 1969.

Figure 19. Percentages of samples in which individual males were at various distances from females. Abscissa is divided into five half-hour intervals (I-V) beginning 10 minutes 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 meters in a neighboring territory (hatched part), or had no females nearby (open part). Data from 27 March - 1 April 1968. Males near a mating center (D, TM, and B) associate with females more often than do other males.

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 center. 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 may not stem entirely from greater chances of 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 center shortly after sunrise, peripheral males Strut much less persistently, whereas males near the mating center Strut steadily as long as females remain, sometimes more than two hours after sunrise.

F. Shifts in the Positions of Mating Centers

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 center. I have discussed these shifts of mating centers in an earlier section. In 1968 when the mating center drifted south-west 8 meters, Male D accompanied it. At first the mating center 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 neighbors 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 which they had used late in the mornings of 31 March and 1 April. Thus, as the pack of females changed its behavior, Male D simultaneously surrendered a portion of his original territory to his neighbors TM and B. He did not displace any male, because he had no immediate neighbor 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.

Females first appear on leks early in the season in loose, wandering groups (Chapter VIII, Section A). The Strutting males approached as closely as possible to these drifting groups of females, usually without intruding far into neighboring 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 5-20 meters apart and occasionally encountered each other. Usually, though, the males near the center 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 appears again in the reoccupation of the occasional vacancies which arise when territorial males disappear. Such vacancies are 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 center of Male A's former territory but still centered 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 neighbors, Males C, S, and SE, none of which extended their territories to include a part of the vacated area. Male C was also a frequent mater, 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 neighbors. 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 neighbors, 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 9ab). 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 neighbor 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 through 12 April. By 22 April, however, Male A was encountering Male B 3-6 meters north of their former zone of Facing-past Encounters (Maps 10ab). So Male B eventually occupied the territory vacated by TM with boundaries essentially intact, and Male A, B's more peripheral neighbor, also moved his boundary closer to 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 I found no other kills.

One might expect that peripheral males would be most vulnerable to predation on a lek. Surprisingly, both of the kills which I did find were fully adult males with long, tapering tail feathers, although yearlings are more likely to occupy peripheral positions. On the other hand, the signs of fatigue which the predominant breeder often showed suggest that these males might become more vulnerable to predators away from the lek during the mating season. Although the predominant breeder in 1967 did indeed disappear, all of the males which 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 center 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 center does react differently to intruding males than do his neighbors. My observations accord with Patterson's (1952) conclusion that most intruders are yearling males. I successfully followed a few which 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 center early in the mating season. Near the pack of females they always assume Collapsed or Sleeked Postures and, therefore, are not so easily distinguished from females as are the 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 may 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. Thus, when a male has a dense pack of females within his territory, he often overlooks intruders among the females until he approaches with 2-3 meters 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 may weave 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 may 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, an orientation that reduces his conspicuousness to his previous pursuers. Although such an orientation clearly reduced the intruder's conspicuousness, 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 in the periphery of the lek, where he goes unnoticed for several minutes, he may gradually assume the Semi-Collapsed or rarely the Strutting Posture.

especially late in the morning (around 8:00), without any signs of localizing their movements. On 31 March, 1, 2, 4, 5, and 10 April I observed the males in an area 50-100 meters north of Mating Center #1. Females first showed signs of clustering at Mating Center #1 on 1 April. On these days just preceding and during the first congregations of females at the mating centers, I could detect nothing unusual in the intensity or frequency of the males' agonistic encounters. In the area north of Mating Center #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 Center #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 meters 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 centers.

Yearling males, as I shall describe presently, establish positions on a lek later in the season than do older males. Perhaps a male's tendency to occupy his position on a lek early in the spring continues to increase with age after his first year, a possibility not yet investigated. For instance, second-year males might not arrive on a lek as early in the season, or as persistently during bad weather, as the third-year males. If the oldest males arrived on a lek earliest

in the spring, or most persistently during bad weather, this behavior should predispose them to obtain centrally located territories. 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.

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 (Chapter XIII, Section A). Autumn display might allow juvenile males and females to experience a lek for the first time at ages of 3-5 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, late comers often flew from the periphery of the lek to their territories. My observations indicated that neighboring males usually did not arrive together either in the morning or in the evening. Lumsden (1968), however, felt that groups of several neighboring 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 Collapsed 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.

never reaches the average for older males, although yearlings apparently do produce spermatozoa. They do not normally participate in the mating, since 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 center. Probably most of the intruding males in Collapsed Posture, which often penetrate to the center of the lek at this stage of the season (this Chapter, Section 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 neighboring adults encountered him. Clearly, his older neighbors even in late April freely chased him from his favored 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 10ab 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 neighbors. The yearling Male Z encountered his adult neighbor 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 April 10 (Figure 1). Other observers have recorded similar increases in the number of

males displaying at leks, owing to the increment of yearling males (Batterson and 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 which 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 10-15 minutes later in the morning than did the older males around the mating center.

To compare the frequencies of Strutting by yearling and older males, I used eight six-minute sequences of time-lapse film from the Fords Creek Lek on several days in late April 1968. Yearling males tended to Strut somewhat more often when no females were nearby than did older males in similar circumstances (Figure 20). 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 this situation. Yearlings spent somewhat less of their time in Facing-past Encounters than did older males with no females nearby (Figure 21).

To recapitulate, yearling males begin displaying regularly on a lek later in the season than do older males. They apparently do not mate in normal circumstances, 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.

Figure 21. Allocation of time to Facing-past Encounters by yearling and older males. 22-25 April 1968.

X. SUCCESS IN MATING

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 center. These two observations suggest a mechanism by which a male might come to occupy a territory at a mating center. If males tend to return to the same lek in successive years and to occupy positions at least as near a mating center 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 center. 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 behavior of grouse at a lek after cannon-netting. Nevertheless, observations of marked birds by Dalke and his colleagues (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: 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 center 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 at least one year old approximates 50% per year (Table 17). Males in their second year perhaps have higher mortality than those in their third and fourth years, but this evidence is not clear (June, 1963). Studies by Dalke and his colleagues (1963) suggest mortality rates even higher than 50% 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.

Estimates of mortality are available for several other tetraonids (Table 18). For instance, mortality rates among color-banded Blue Grouse (Dendragapus obscurus) range from 25% to 31% per year in unhunted populations on Vancouver Island (Bendell and Elliot, 1967; Zwickel and Bendell, 1967), while in a hunted population in Alberta the rate is 56% per year (Boag, 1966). Bendell and 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 25-50% per year, transposition of a surviving male into a mating center might require only a few years. This mechanism implies that the more central 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 yearling females virtually all breed (Chapter VIII, Section A). If my hypothesis concerning the centripetal movement of males' territories is correct, two-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 center might increase steadily with his age. Present evidence cannot specify whether this probability approaches 1.00 at some age.

To recapitulate, my observations suggest that during their life-span males migrate centripetally within a lek as vacancies arise toward the mating center. So polarity in the territorial behavior of the males probably would correlate at least in a rough way with radial differences in the males' ages. Attainment of success in mating would then be an ontogenetic process, which begins when a yearling establishes his territory at the periphery of a lek. The social organization of a Sage Grouse lek would depend on polarized interactions between males usually of different ages.

Table 18
Estimates of annual adult mortality rates in grouse and pheasants based on studies of banded populations

Species (Location)	Hunting	Annual Adult Mortality ⁽¹⁾	Mortality in Second Year of Life Compared with Later	Sexes Differ	References
Red Grouse, <u>L. lagopus</u> (Scotland)	+	65%	Same	No	Jenkins, Watson, Miller, 1967
White-tailed Ptarmigan, <u>Lagopus</u> <u>leucurus</u> (Montana)	-	29%	?	Territorial males perhaps lower = 20%	Choate, 1963
Blue Grouse, <u>Dendragapus</u> <u>obscurus</u> (Vancouver I.)	-	26-31%	Same	No	Bendell and Elliott, 1967
(Alberta)	+	56%	Same	No	Boag, 1960
Ruffed Grouse, <u>Bonasa umbellus</u> (Minnesota)	(2)	50-60%	Same	Females slightly higher than males	Gullion and Marshall, 1968
Capercaillie, <u>Tetrao urogallus</u> (Finland)	+	40%	?	?	Helminen, 1963
Black Grouse <u>Lyrurus tetrix</u> (Finland)	+	80%	?	?	"
Ring-necked Pheasant <u>Phasianus sp.</u> (Wisconsin)	?	50-80%	?	?	Reviewed by Hickey, 1955; Farner, 1955

(1) Annual mortality of birds after the first year of life.

(2) In hunted areas mortality slightly higher than in protected areas.

male intruded more than a short distance into his neighbors' territories to interrupt their matings. Inhibition against intrusions was particularly evident when a vacancy remained unoccupied for one or two days after the disappearance of the original occupant.

Encounters between neighboring males apparently function in establishing the locations of boundary zones between territories rather than in deciding classical dominance-subordination 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", since encounters essentially never result in a polarized outcome. The male initiating an encounter usually terminates it; when an encounter terminates, both contestants return to their respective territories. Within the usual boundary zone Facing-past Encounters virtually never shift position more than a meter. When a Strutting male transgresses the boundary zone, he usually quickly retreats to the boundary zone after the resident male initiates an encounter. First-year males, in contrast, do get chased long distances by neighboring 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 neighbors.

Like many other territorial birds, male Sage Grouse occupy territories separated by narrow, mutually recognized zones, within which neighbors encounter each other as equals. Within his own territory a male Sage Grouse is dominant, and the dominance relationship of two neighbors reverse within a boundary zone which is often only one or two meters wide. The aggression gradient of a territorial male Sage Grouse, therefore, resembles a Type A gradient, one in which each male's capacity to dominate agonistic encounters remains maximal until it decreases steeply in a narrow boundary zone (Chapter II; Figure 1). Although a male's territory is largely exclusive with respect to other

territorial males, the exclusion gradient does not decrease across the territorial boundary quite as steeply as does the aggression gradient. In other words, territorial males occasionally encroach beyond the boundary zone in which neighbors meet as equals in Facing-past Encounters. In many respects, therefore, the behavior of male Sage Grouse conforms to the classical pattern of territoriality.

Nevertheless, territoriality in male Sage Grouse diverges from the classical conception in having certain polarized, or non-reciprocal, features, as well as reciprocal features. The interactions of territorial males nearer a mating center with those farther away lack reciprocity in the initiation and termination of Facing-past Encounters between neighbors and in the occupation of vacancies. In all of these cases, the polarized interactions of radial neighbors apparently originated in the attractiveness of the mating center for the territorial males. Territorial males nearer a mating center apparently inhibit the occupation of these areas by males established in more peripheral positions. Furthermore, the behavior of males nearer a mating center differs in several respects from the behavior 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 center also usually occupy smaller territories. In effect, the territories show hierarchical ranking. Present evidence indicates that occupation of a territory near a mating center should correlate roughly with increasing age.

Lumsden (1968) has suggested that male Sage Grouse could maintain a 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. However, since I could not confirm his conclusion that the males arrived and left together each morning, I feel uncertain that the males around each mating center remain together when away from the lek.

The size of a territory results from the interaction of external pressure applied by territorial neighbors and internal resistance exerted by the territorial resident. Since the more central males devote less time to agonistic encounters than do their more peripheral neighbors, the efficiency of their resistance might not equal that of more peripheral males. Furthermore, external pressure on central territories might be greater than on more peripheral ones. If the attraction of the mating center for territorial males decreased at increasing distances, males established at greater distances from the mating center might well exert less pressure on their more central neighbors.

The reoccupation of vacancies on a lek presents an unresolved problem. Which of two neighbors equally distant from a mating center will occupy a vacancy arising closer to the mating center? In two cases a vacancy had two or more neighbors equally distant from the mating center. 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 which included part of a mating center, his three neighbors Males N, SE, and S seemed equally likely to reoccupy the vacancy. Male A's fourth neighbor, Male C, already occupied a portion of the area in which matings occurred frequently. At least in this second case, following the disappearance of Male A, none of the three neighbors immediately occupied the vacancy. Not until three days later was Male N using the vacated area extensively, encountering the other three neighbors 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 neighbors to reoccupy the vacancy. Perhaps differences in the males' ages would give

XII. INDIVIDUALITY IN THE INTERACTIONS OF MALES

A male Sage Grouse on a lek has one clear source of individual identification: his location. The position of a male's small territory identifies his rank in the hierarchy of territorial males. 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 neighbor arrives later than he does.

Whether or not 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 behavior changed remarkably little when a former neighbor disappeared and a new neighbor 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 neighbor, Male UT, remained unchanged, the behavior 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 (Figure 17; 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 the strict localization of each territorial male, Sage Grouse do not have clear sources of individual identification. Their displays and acoustic signals, as a result of extreme species-specific stereotypy, show only slight individual differences among males at least two years old. In contrast, the acoustic signals of many other birds do contain information which clearly identifies the

individual (Marler, 1960; Weeden and Falls, 1959; Falls, 1969; Thorpe, 1968).

Individual recognition is probably not necessary to maintain hierarchical organization among individuals. Instead, individuals might discriminate among classes of other individuals. An individual in a hierarchy might not discriminate among all other individuals in the hierarchy, but only between 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 have to recognize individuals with higher and lower aggressive tendencies, for instance, by their longer or shorter critical distances for initiating an attack.

These considerations suggest that the hierarchical organization of territorial male Sage Grouse might depend more on the spatial localization of individuals than on individual recognition independent of location. Male Sage Grouse apparently have not evolved any features of plumage or behavior that would clearly facilitate individual identification.

Descriptions of the territorial behavior of males appear in almost all accounts of lek behavior of these species: Black Grouse (Selous, 1909-1919; Lack, 1939; Höhn, 1953; Kruijt and Hogan, 1967; Koivisto, 1965); Capercaillie (Lumsden, 1961); Prairie Chicken (Hamerstrom, 1939; Hamerstrom and Hamerstrom, 1955, 1960; Schwartz, 1945; Robel, 1941); Sharp-tailed Grouse (Lumsden, 1965; Evans, 1969). 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 about 30 square meters in area (Lumsden, 1965). In Prairie Chickens the smallest territories are about 75 square meters (Hamerstrom and Hamerstrom, 1960). In Black Grouse the smallest territories which Lack (1939) observed were about 35 square meters. However, Kruijt and Hogan (1967) found none less than 100 square meters in area. Male Prairie Chickens and Sharp-tailed Grouse frequently leave their territories to approach females on the lek (Lumsden, 1965; Hamerstrom and Hamerstrom, 1960; Robel, 1964). In contrast, Black Grouse males usually remain within their territories when females are on the lek (Höhn, 1953; Kruijt and Hogan, 1967; Hamerstrom and Hamerstrom, 1960). Most copulations are performed by males at least two years old established near the center of a lek (Robel, 1967; Koivisto, 1965; Kruijt and 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 ranges of the individual males on a lek by plotting their positions at 15-minute intervals. Other observers have determined territory sizes from the positions of the agonistic encounters between neighbors. Apparently the central males, which mate most often, leave their territories when females visit the lek.

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 and Hamerstrom, 1960;

Koivisto, 1965; Evans, 1969) 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 meters into the center of the lek to occupy a vacancy. This is exactly the behavior expected on the basis of my observations of Sage Grouse.

Many studies have mentioned the peripheral positions and less constant attendance of yearling males (Lumsden, 1961; Lack, 1939; Koivisto, 1965; Kruijt and Hogan, 1967; Robel, 1967). Yearling male Black Grouse may penetrate the center of the lek as intruders (Koivisto, 1965; Kruijt and 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 (Kirikov, 1947; Lumsden, 1960). In addition, Kirikov (reviewed by Dementiev and 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 two-year-olds began displaying first but not so early in the season as the older males had. If he removed the two-year-olds as well, then yearlings occupied the center of the lek. Studies of other lek-forming species of grouse apparently have not compared the seasonal course of display by yearling and older males, nor the growth of yearling and older males' testes.

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

and White-tailed Ptarmigan (L. leucurus) also usually form monogamous pairs, although occasionally two females will settle in one male's territory. However, the association of a mated pair seems to dissolve during or shortly after incubation (Choate, 1963; Watson, 1965; Dementiev and Gladkov, 1967; Weeden, 1965). The pair-bond in Hazel Grouse seems to resemble that in Rock Ptarmigan. In both species the bond forms before incubation begins, but males rarely accompany the female and her brood (Pynnönen, 1954; Fuschlberger, 1956). At least in the White-tailed Ptarmigan, among these usually monogamous species, yearling males maintain smaller territories and often do not mate (Choate, 1963).

Promiscuous Grouse which do not form leks. The remaining four species of grouse apparently do not form durable pair-bonds, since most reports suggest that males and females do not remain together at any stage of the breeding cycle. Movements of female Blue Grouse Dendragapus obscurus and Ruffed Grouse Bonasa umbellus are not confined to one male's territory (Bendell, 1958; Bendell and Elliot, 1967; Boag, 1966; Brander, 1967). However, Blackford (1963) observed a stable association between a pair of Blue Grouse, even though the female often left the male's territory. Displaying male Blue Grouse, Ruffed Grouse (Bump et al., 1947; Gullion et al., 1962; Gullion, 1967), and Spruce Grouse Canachites canadensis (MacDonald, 1968) disperse themselves more or less evenly throughout the habitat. Blue Grouse males defend an area around their display site by chasing or fighting intruding males (Bendell and Elliot, 1967). Many yearling males of this species do not establish display territories. The yearlings have smaller testes, shorter tails and weigh less than older males (Bendell, 1955, 1968; Swarth, 1926).

The best evidence for ranking among territorial male Sage Grouse is their tendency to shift their territories as vacancies arise in more advantageous locations. This sort of polarity in the interactions of males seems absent in Blue Grouse. Once a male has established a display territory he returns to that territory in successive years as long

as he survives (Bendell and Elliott, 1966, 1967). Ruffed Grouse males do often change their display sites if they survive several years, but the factors which influence the choice of a new site remain unknown (Gullion, 1967). Bendell and Elliot (1967) investigated the effects of removing territorial male Blue Grouse during the breeding season. When they removed males from 31 territories, less than a third of which were yearlings, only 13 (42%) of these territories were reoccupied that season. Two-thirds of the new males were yearlings. If displaying male Ruffed Grouse are removed, only a minority of the display sites are reoccupied that season and these by yearlings (Dorney and Kabat, 1960). So the removal of displaying males in both of these species allows some yearling males to establish themselves, but many vacancies remain unoccupied at least until the following year.

Some display sites are used by a succession of males, so that these sites have traditional locations. Bendel and Elliot (1967) present evidence that displaying male Blue Grouse attract yearlings to their territories. These yearlings might occupy these sites in the following year if the usual occupant failed to return. Ruffed Grouse display sites also attract yearling males. A yearling may regularly frequent the vicinity of a traditional display site, yet rarely display. On several occasions when the regularly displaying male disappeared, such a yearling reoccupied the vacated display site (Gullion, 1967).

Nothing is known about the dispersion of matings among males in these species, owing to the difficulties of observing widely dispersed birds in forested habitats. In particular, it remains unknown whether traditional sites, those occupied by a succession of males, offer advantages for mating. In both species essentially all yearling females breed, although apparently many yearling males do not, so polygyny might result.

mate (Nero, 1956; Selander and Giller, 1960; Orians, 1961; Wright and Wright, 1944). The testes of yearling males grow later in the season and average smaller than older males' (Wright and Wright, 1944). If the adult territorial males in a nesting marsh are repeatedly collected, eventually some yearling males establish territories in the areas previously occupied by older males (Orians, 1961). So the lower breeding success of yearling males in this species might result both from intrinsic physiological differences and from social interactions between younger and older males. Selander and Hauser (1965) have described similar differences in the patterns of gonadal growth and behavior in yearling and older male Great-tailed Grackles Quiscalus mexicanus. In general among polygynous species, males first mate at a later age than do females and yearling males do not acquire fully adult male plumage (Selander, 1965; Crook, 1964), yet the changes in male behavior with age and the interactions among younger and older males have received little attention. In polygynous species when the opportunities for mating differ with the locations of the males' territories, polarized interactions might characterize the territorial behavior of the males.

D. Polygyny in Mammals

Delayed breeding among males in comparison with females and lack of male parental care occur in polygynous mammals as well as birds. In most mammals other than certain carnivores, the females provide most of the energy required for fetal growth and parental care. The reduced contribution of the male to parental care correlates with more frequent polygyny among mammals than birds (Orians, 1969). A few examples will illustrate the occurrence of delayed breeding among males in species in which copulations are not randomly distributed among males.

The polygynous pinnepeds offer some striking parallels with lek-forming grouse. Species like the elephant seals (Mirounga spp.) (Bartholomew, 1952; Carrick et al., 1962a, b) and northern fur seals Callorhinus ursinus (Bartholomew and Hoel, 1953; Peterson, 1968) gather for breeding in large colonies on oceanic islands. Here the females

congregate in dense "harems" around large bulls, which occupy positions near the shore. Bull northern fur seals defend sharply delineated territories against intruding males, while bull elephant seals apparently exclude other males from the herds of females but do not defend fixed boundaries. The females come ashore shortly before parturition. After giving birth to their single pup they spend several weeks (elephant seals) or months (fur seals) suckling the pup either with (fur seal) or without (elephant seals) periodic trips to sea for feeding. Female northern fur seals enter estrus about six days after parturition just before leaving for their first excursion to sea, while female elephant seals copulate in the third week following parturition and a few days before deserting their well-fed pup. Since the gestation period is about eight to nine months, parturition and fertilization are brought into seasonal proximity by delaying implantation of the blastocyst for several months. Thus although pinneped rookeries represent aggregations of animals for the purposes of mating, like the leks of grouse, parturition and parental care also occur in the rookery. Some polygynous pinnepedes probably occupy most of the appropriate shoreline in their small breeding islands, so that the animals appear not to have congregated at particular sites within the suitable habitat. In other species, though, published accounts definitely suggest that pinneped rookeries do constitute true social clusters (Callorhinus ursinus, Kenyon et al., 1954; Zalophus, Peterson and Bartholomew, 1952). Polygyny is associated with the formation of harems, or clusters of females, around breeding males. The breeding bulls in several species attempt to prevent females from leaving their harems by herding the females or chasing them back when they begin to wander away or, rarely in the northern fur seal, by bodily throwing the female toward the center of the territory. Early accounts (Allen, 1880) apparently exaggerated the males' influence on harem formation, though. Several authors have noted that males cannot prevent females from leaving their harems if the female chooses to go (Halichoerus, Darling, 1939; Mirounga, Bartholomew, 1952; Callorhinus, Bartholomew and Hoel, 1953; Peterson, 1968; Arctocephalus,

Macquarie respectively), the average number of females controlled by breeding bulls is smaller on South Georgia (24 in contrast to 48 on Macquarie) (Carrick et al., 1962b). In response to the heavy, induced mortality of older males, both males and females breed at younger ages.

Male and female fur seals also differ greatly in the onset of successful reproduction. In the Pribilof Islands females normally bear their first young at age five, while in a sample of 199 territorial males the youngest was one male seven years old (Johnson, 1968). Most males do not establish territories until they are 9 to 11 years old (Kenyon et al., 1954).

Males of polygynous artiodactyls also reproduce successfully at later ages than females. For instance, cow Tule Elk Cervus elaphus nanodes mate for the first time in their first or second year of life, whereas bulls are clearly older before they manage to defend exclusive access to a cow herd during the rut (McCullough, 1969). This author recognized one bull in two successive years, and this animal improved his mating success in the second year. Among North American mountain sheep (Ovis dalli, O. canadensis) the dominant males, which have the largest horns, copulate with most of the females (Geist, 1966, 1968). Instead of defending an entire band of females, as dominant bull elk do during the rut, a dominant ram instead tends one female at a time as they come into estrus. Most ewes copulate first when about 2½ years old, but rams do not grow full-sized horns, nor normally copulate successfully, until they are 7 or 8 years old. The older and larger males of some antelopes (Bovidae) isolate themselves during the rut in territories from which they exclude other males. In their territories they court and copulate with females, which wander from territory to territory in groups. The Uganda kob Adenota kob has developed an extreme form of this type of social organization. Males occupy small (15-35 meters in diameter), contiguous territories which cluster around particular sites two to three kilometers apart in favorable savanna habitat in Uganda (Buechner, 1961; Buechner and Schloeth, 1965;

Leuthold, 1966). These clusters of small territories, called Territorial Grounds, resemble the leks of grouse in that almost all mating activity occurs there. Other male kob maintain much larger (100-200 meters in diameter) territories, called Single Territories, in the zones between the Territorial Grounds. However, copulations do not normally occur in these larger territories, since the estrous females usually visit the Territorial Grounds for mating. Consequently, male kob compete less intensely for the larger Single Territories. Males established near the center of a Territorial Ground remain on their small territories constantly for several days until they must leave to feed, since these small territories do not include enough food for the males to maintain themselves indefinitely. Thus the occupants of the territories rotate every few days as males in poor condition leave to feed elsewhere and returning males replace them. This rapid turnover of territorial occupants does not occur on grouse leks, because in these species all the males leave their lek for at least nine hours each day to feed. The age-distribution of male kob on Territorial Grounds and on Single Territories does not differ significantly (modal ages respectively 5 and 4 years) (Leuthold, 1966), although most of the mating occurs on Territorial Grounds. The relationships between males on Territorial Grounds and those on Single Territories remain uncertain, however. Leuthold (1966) reports that, although most males during their absences from Territorial Grounds join "bachelor" herds, at least some individually marked males occupied Single Territories temporarily before returning to the Territorial Ground. Also most copulations are performed in the central territories on a Territorial Ground, another resemblance to grouse leks, but Leuthold's (1966) age determinations for males collected on Territorial Grounds did not differentiate central and peripheral males. The behavioral cycles of individual male kob and the interactions between males of different ages require further study. Females first mate between 1 and 2 years of age, while males probably do not successfully copulate until they are 3-5 years old (Buechner et al., 1966).

find no careful assessment of the effects of age on dominance, or of the changes in individuals' ranks with age. The rank of an individual's mother often appears to influence an animal's own rank even more than age does (Koford, 1963; Sade, 1967; Kawai, 1958; Kawamura, 1958). Females especially tend to rank just below their mothers in the troop's dominance hierarchy. Males do not retain such close associations with their mothers, yet the sons of high-ranking females sometimes reach high rank among the troop's males when only 5 or 6 years old (Koford, 1963). Thus the determinants of dominance and mating success among male macaques seem to involve complexities not found in animals other than primates. Nevertheless, it seems clear that females begin reproduction regularly at an earlier age than do virtually all males.

XIV. PROBLEMS IN THE EVOLUTION OF LEK MATING SYSTEMS

In preceding sections I have drawn attention to several general features of leks and other polygynous mating systems in birds and mammals. These features include (1) non-random distribution of matings among adult males, (2) reduction in or lack of male parental care, and (3) onset of successful reproduction at a later age in males than in females; leks are in addition characterized by (4) aggregation for the purposes of mating. The present section will consider the evolution of these features of polygynous mating systems. In this discussion fitness (Dobzhansky's (1969) "Darwinian fitness") denotes the rate at which an individual's genes propagate in subsequent generations, relative to the rates at which other individuals' genes propagate. Adaptedness (adjectival form, adaptive) refers to the relation between an organism and its environment, on which fitness depends. Fecundity means the number of reproducing offspring.

A. Delayed Reproduction Among Males

Selander (1965) has reviewed evidence that in polygynous species of Icteridae (blackbirds, grackles and allies) males usually first breed successfully at a later age than females. He points out that among Icteridae first-year males do not have fully adult plumage and their testes do not reach the size of older males', so first-year males in comparison with older males are handicapped in their chances for mating by their less developed plumage and their presumably lower androgen titers. In analogy with Lack's (1954) explanations for delayed reproduction by both sexes in certain monogamous species, Selander proposed that postponed breeding by males in polygynous species can be explained by combining two considerations: (1) year-old males have less chance of successfully mating in competition with older, more experienced males, and (2) year-old males would increase their risks of mortality by assuming full breeding plumage and competing for territories and matings. In a more quantitative analysis of Lack's suggestion, Williams (1966)

later ages does not alone compensate for the delay in the onset of reproduction. This is not to imply that delayed reproduction will inevitably result in decreased fitness. Gadgil and Bossert's (1970) and W. M. Schaffer's (MS) calculations suggest that the two conditions which Selander, Williams and Lack originally suggested, when sufficiently large, could indeed favor delayed reproduction: high risk of mortality during reproduction and fecundity increasing with age. Stated differently, if a young male by reproducing so jeopardizes his chances of survival to the following breeding season and yet gains a sufficiently small chance that two of his progeny would survive to reproduce, then by breeding at an early age a male might actually reduce the chances that his genes would remain in the population.

The arguments so far suggest (1) that in determining a male's fitness the increase in average fecundity of polygynous males at later ages will not in itself compensate for their postponement of reproduction, but (2) that with sufficiently large risks to survival as a consequence of reproduction as well as with increasing fecundity at later ages, males might indeed optimize the rate of spread of their genes by postponing the onset of breeding.

The proximate regulation of postponed breeding might involve several factors: (1) direct prevention of younger males' attempts at mating by older males; (2) physiological immaturity which precludes mating by younger males even in the absence of older males, owing to inadequate development of secondary sexual characters and inadequate motivation to attract and elicit copulations from females; (3) indirect prevention of younger males' matings by social dominance of older males, which might thereby obtain priority to territories favored by females; or (4) "psychological castration" (Guhl *et al.*, 1945), an interaction of processes (2) and (3), by which full physiological development of gonads and secondary sexual characters is inhibited in subdominant individuals. To my knowledge, no full evaluation of these four possibilities is available for any polygynous species. At least in

None of these physiological or behavioral processes explains the adaptedness of the males' delayed breeding in comparison with females in polygynous species. The theoretical considerations which I have reviewed implied that delayed reproduction would most likely improve fitness if potential fecundity increased sufficiently with age and early reproduction sufficiently jeopardized survival. Epigamic and parental behavior and morphological specializations might increase mortality in several ways: (1) by reducing the time and energy available for predator avoidance, maintenance, feeding, resting; (2) by increasing the conspicuousness or vulnerability of individuals to predators; or (3) by injuries incurred during intraspecific competition for mates. Thus, intraspecific competition for mates might increase the risks of mortality either directly through injuries, or indirectly, through the effects of epigamic behavioral and morphological specializations on interspecific interactions with predators, food supplies, or competitors.

Although there is no direct evidence that male Sage Grouse improve their chances of survival by postponing breeding, some indirect evidence suggests this could conceivably happen. Yearling males certainly spend less time and energy on a lek than do older males, since yearlings arrive later in the season than do older males and rarely display as persistently as older males with females near them. The energy and time they conserve might increase the yearling males' chances of survival, for instance by allowing more time for feeding. Even among the older males, the more peripheral ones probably expend less energy on a lek, since they spend less of the morning Strutting. Peripheral males never showed the occasional signs of fatigue observed in the predominant breeder late in a morning when females had been numerous. Strutting must be strenuous exercise for a male. The 7-10 second interval between Struts might just allow sufficient recovery to permit long-sustained Strutting. The central male with the most sustained close association with females occasionally Strutted at unusually low rates late in the morning, a probable indication of his fatigue. However, satiation, rather than fatigue, could also explain this lethargic behavior late

in a morning after much display and mating.

One might expect that yearlings, usually the most peripheral males on a lek, would incur greater risks of predation, since attacking predators would first contact the periphery of a lek. Yet, the only two kills which I found on leks involved males in at least their second year. The kill by a Golden Eagle on the Muddy Springs Lek in 1968 occurred near the center of the lek, roughly 50 feet from the mating center. The risks of predation at different positions on a lek need further investigation.

The direct consequences of competition among males for opportunities to copulate appear to have little effect on survival. I never saw a male sustain an injury in a fight, although fighting clearly might have indirect effects on survival since it represents an appreciable expenditure of energy. It is not even clear that the males' positions on a lek were primarily determined by fighting.

Younger males among Sage Grouse and probably other polygynous species appear, on the basis of incomplete and indirect evidence, to have reduced some of the indirect effects by which intrasexual competition for mates might reduce survival. My impression is less that older males prevent the younger from mating than that the younger invest less effort in competing for matings. In many polygynous species the reduced "effort" of younger males is manifested not only in less energetic and persistent behavior but in assuming less conspicuous or encumbering secondary sexual characters or in not growing to the full size of older males.

It would be over-simplifying to assert that the younger males exert less effort merely because they are not likely to succeed against or might get injured by the older and often larger males. This formulation would leave unanswered the question of why the males did not develop full reproductive capacity, including full gonadal growth and secondary sexual characters, at an earlier age, as do females of the same species. I have tried to suggest that the propagation of a male's

copulate even without investing as much time and energy as older and more successful males. Since age at first breeding so strongly influences the rate of spread of a gene, selection might favor investing some energy for reproduction at an early age even if the chances of success were very small. For year-old male Sage Grouse the chances for copulating seem almost absent. (2) Partial development of adult male morphology might aid an individual in agonistic interactions other than competition for mates. I have found no evidence for this possibility in Sage Grouse. (3) Some time and energy spent at a young age might improve the male's opportunities for future success. Selander specifically suggested that experience gained as a yearling might improve a male's ability to compete for mates in later years. In Sage Grouse if the hypothetical centripetal movement of territories proves correct, effort expended by first-year or older peripheral males might indeed enhance their future success in at least two ways. In order to attain success in mating, a male would have to start the process which leads, by the occupation of successive vacancies, toward a mating center. Furthermore, if leks with more males attract more females and if females tend to return in successive years to the same lek, then by displaying in a peripheral position a male might actually increase the number of females with which he will have a chance to mate in later years. It would then be adaptive for a yearling male to commit himself to a particular lek and expend some energy, although presumably not so much as the older males, in attracting females to the lek.

B. Intrasexual Competition

Although I have suggested that reduced reproductive effort among younger males should be adaptive for reasons other than competition with older males for mates, intrasexual competition might still constitute a critical selective force among the older males. As reproductive success increases with the males' ages, some age might be reached at which essentially all males became equally successful breeders; or, conversely, large inequities in the distribution of matings might remain

at all ages. In the first case, the coefficient of variation of fecundity among individual males would fall to a small value with increasing age, while in the second case it would remain high. The first case does not differ appreciably from the situation which probably characterizes most monogamous species in which the majority of males each obtains one mate. Yet in polygynous species, even if the variance in fecundities among individual males does approach some small value with advancing age, there always exists the potential for competition among males for opportunities to mate.

Intrasexual competition for mates can occur in two guises, as Darwin (1871), Huxley (1938), and Fisher (1958) describe. On the one hand, agonistic interactions among males might determine which males have access to females. The object of competition in this case might be a territorial location to which females are attracted, a position in a herd of females, or high rank in a dominance hierarchy. Alternatively, interactions between males and females might determine which males are chosen by females as mates. These two forms of intrasexual competition actually represent two poles of a continuum: males vie with each other either to attract and stimulate females directly, or to hold positions that attract females or that increase accessibility to receptive females.

The mating system of Sage Grouse probably depends on critical interactions among males, between males and females, and among females. The context of intrasexual competition for mates is, therefore, not simple. I have suggested that females might remember at least the approximate locations of mating centers on leks and return to them on subsequent visits; also that on their first visit females might recognize the mating center partly by the dense aggregation of other females there. Perhaps some as yet unrecognized male-female interactions might also affect the distribution of matings among the males near a mating center. Nevertheless, my observations suggest that interactions among the females could specify the locations of the mating centers. This would imply that males compete primarily for

as on male-female interactions. Once harems have formed males established in peripheral positions tend to expand or move their territories as much as possible toward the areas favored by females (Kenyon, 1960).

C. Evolution of Female Behavior

My observations failed to reveal evidence that female Sage Grouse chose a place to copulate by discriminating individual differences in the behavior of the males. Although undetected influences of individual differences among males might exist, females appear to base their choice partly on tradition among the females themselves. In another polygynous bird, the Long-billed Marsh Wren, females appear to choose a nesting site on the basis of habitat quality rather than the males' behavior (Verner, 1964). Although the proximate mechanisms of female choice do not necessarily involve discriminations among individual males, these proximate mechanisms should evolve to maximize a female's changes of mating with fit males as well as to maximize her fecundity.

A male's fitness, as I have discussed above, consists not only in his ability to compete successfully with other males for mates, but also in the optimal allocation of his time and energy throughout his life cycle to reproduction or to maintenance and growth. Unless a male life history with delayed reproduction maximized the spread of a male's genes, a female's genes would propagate faster if she selected a younger male and left sons that would also tend to breed at an early age. In other words, females should not restrict their matings with young males unless early breeding by a male decreases his fitness. To understand the evolution of females' behavior we must understand the adaptive significance of the males' life history and behavior. An assertion that females mate with older males because these have demonstrated their ability to survive (for instance, Robel, 1967; Koivisto, 1965) assumes that male fitness consists in survival, an assumption that is only partially true. Similarly, an assertion that a male's fitness consists in the number of females with which he mates also is only partially correct, since reproductive rate depends not

only on average fecundity but even more on the age of breeding and also on the consequences which breeding at a given age have for expectations of future reproduction.

D. Genetic Diversity

The Sage Grouse exemplifies an extreme form of non-random mating, in which only a few percent of the males copulate with most of the females. This distribution of matings might effect genetic diversity in two ways: by reducing the effective population size, and by producing strong normalizing selection in favor of those genotypes which could eventually reproduce successfully. When the two sexes are unequally represented among breeding individuals, the effective population size is less than when the sexes are equally represented. The effective population size was shown by Sewall Wright (see Falconer, 1960) to equal twice the harmonic mean of the numbers of the two sexes:

$1/N_e = 1/4N_m + 1/4N_f$. Letting N_b equal the total number of breeding individuals and p equal the proportion of males among this total, then $N_e = 4p(1-p)N_b$. If males comprise 5% of the total number of breeding individuals, the effective population size approximates 19% of the total number of breeding individuals. Thus from the standpoint of random dispersive processes in their gene pools Sage Grouse populations should behave like much smaller populations in which equal numbers of both sexes breed. Exact calculations of the ratio N_e/N_b for Sage Grouse are not yet possible, since available mathematical treatments do not take into account overlapping generations or unequal participation by breeding males in mating. In order to calculate N_e one must also know the total number of breeding individuals in the population. Although breeding individuals probably tend to return year after year to the same lek, there is probably much less correlation between the leks used by parents and their progeny (this Chapter, Section F). Thus the total number of individuals in an interbreeding population of Sage Grouse is likely to be larger than the number of males and females which mate at any particular lek.

as a function of age. In some circumstances delayed reproduction might evolve. Armstrong (1955), Snow (1963), and Crook (1965) suggest that superabundant food supplies might allow females to raise their broods successfully unaided by a mate, and that reduced male parental care should then predispose a species to polygyny. However, they suggest that, once males are relieved of parental duties, polygyny would evolve solely as a consequence of competition among males for mates, rather than, as I have suggested above, as a consequence of adaptive readjustments in the expenditure of reproductive effort by males as a function of age.

F. Aggregation of Displaying Males

Aggregation for mating constitutes an important attribute of a lek mating system, and several authors have considered the adaptive consequences of the aggregation of displaying males. Most of their suggestions are not mutually exclusive, so that a number of them might prove correct. The suggestions fall into four principal categories: (1) consequences for predation; (2) increased stimulation of females; (3) population control; and (4) formation of reproductively isolated demes.

(1) Aggregations of animals have two counteracting effects on the risks of predation. On the one hand, an aggregation probably is easier for predators to detect, particularly if it includes individuals engaging in conspicuous behavior or having conspicuous color patterns. On a Sage Grouse lek, much of the males' behavior serves in part to advertise the lek to conspecific males and females. However, predators must also be attracted. Furthermore, the traditional locations of leks should render them especially susceptible to a predator that can remember their positions. Golden Eagles seem particularly likely to harass Sage Grouse leks, although I could not ascertain whether individual eagles tended to visit the same lek on different days. The eagles' behavior clearly indicated that they attempted serious attacks on Sage Grouse leks (Chapter IX, Section I). On the other

hand, an aggregation of individuals probably offers advantages in detecting approaching predators (Koivisto, 1965; Lack, 1968). Sage Grouse leks seem to have this consequence also. Balancing their apparent harassment by eagles, leks seem to offer clear advantages in detecting an eagle's approach. A lone male approached from behind might fall easy prey, since the eagles attacked at high speed close to the ground in the dim light of dawn. In a congregation at least one male might detect the eagle and alert the others by flushing. Koivisto (1965) described raids by Goshawks Accipiter gentilis against leks of Black Grouse. He too feels that the aggregation of displaying males offers them some mutual protection. Raptors killed male Prairie Chickens at their leks on the average less than once every 400 mornings of observation (Berger et al., 1963).

(2) Social stimulation within aggregations of breeding animals might provide tonic facilitation of successful reproductive behavior. This possibility, originally formulated by Darling (1938), has recently been discussed by Lehrman (1959) and Orians (1961). The aggregation of displaying males at leks could exert several sorts of tonic influences on female breeding behavior. For one thing, larger congregations of displaying males might attract females disproportionately more than smaller ones would (Snow, 1963; Braestrup, 1966). Estimates of the numbers of copulations on Sage Grouse leks in any season are difficult to obtain. Mating activity varies greatly from day to day, and a majority of the matings occurs on only three or four days of each season (see Chapter V, Section E). Two studies of lek-forming species have attempted to compare the number of copulations per male on leks with different numbers of males (Hamerstrom and Hamerstrom, 1954; Koivisto, 1965). The Hamerstroms' extensive observations of Prairie Chicken leks at the height of the mating season in Wisconsin suggest that neither the average number of females per morning nor the average number of copulations per morning increases in proportion to the number of males on a lek. However, as these authors themselves indicate, their data might not accurately estimate the frequency of copulations

choosing a lek during their first breeding season. Dalke et al. (1963) present evidence that yearling male Sage Grouse often visit more than one lek in a season. Female Sage Grouse probably often nest at considerable distances from the lek at which they had mated (Dalke et al., 1963; Patterson, 1952). Since broods disperse in the autumn, a female's progeny would probably not overwhelmingly return to the lek at which their mother had mated.

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XVI. APPENDIX: RATES OF REPRODUCTIVE INCREASE FOR

MALES OF POLYGYNOUS SPECIES

To calculate the rate of reproductive increase, r , of males I used the standard equation (Andrewartha and Birch, 1954),

$$0 = 1 - \sum_{x=0}^{\infty} e^{-rx} s_x b_x, \quad (1)$$

where x is age, and s_x and b_x are respectively the age-specific survival and fecundity. If J_m equals the probability that a male zygote will survive to age one, and s_m equals the annual survival of males after age one, then s_x for males equals $J_m s_m^{(x-1)}$. I assumed that for polygynous species the fecundity of a male is proportional to the number of females with which he mates. The average fecundity of breeding males is then proportional to the ratio, (number of breeding females)/(number of breeding males). Assuming constant annual recruitment to the population this ratio will equal

$$\frac{\sum_{x=a_f}^{\infty} J_f s_f^{(x-1)}}{\sum_{x=a_m}^{\infty} J_m s_m^{(x-1)}} = B, \quad (2)$$

where J_f and J_m are the probabilities of survival to age one for females and males, a_f and a_m are the ages at onset of breeding for females and males, and s_f and s_m are the annual survival rates after age one for females and males. In addition, I assumed that each male had zero fecundity until age a_m and that all males aged a_m and older shared the breeding females equally, so in equation (1) $b_x = 0$ when $x < a_m$, and $b_x = B$ when $x \geq a_m$. In practice the summations in equations (1) and (2) were carried to the smallest integer value of x at which $J_m s_m^{(x-1)} < .0001$ and $J_f s_f^{(x-1)} < .0001$. By setting the production of sons by a breeding male equal to B and $J_f = J_m = 1$, I assumed that each breeding

Table 19

Rates of reproductive increase of males (r) when adult male and female annual survival rates are the same ($s_m = s_f$) and females begin breeding at age one ($a_f = 1$).

	Age at first breeding among males, a_m			
	1	2	4	8
Adult annual survival rates, $s_m = s_f$				
.1	.095	.050	.026	.013
.5	.405	.248	.143	.080
.9	.642	.436	.283	.176

XVII. MAPS

19-25 April 1967

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 two years old (capital letters), 3-5 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 one to three meters wide (see Maps 8b, 9b). Stars indicate positions of marker flags on a 50-foot (15.4-meter) 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 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.

1 April 1968, 0545-0630

- ○ Matings
 ⊗ Interrupted matings

1 April 1968, 0630-0810

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 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, 3-5 April 1968. Boundaries indicated by solid lines are based on Facing-past Encounters in Map 8b. See Map 5a for explanations of symbols.

Map 9a. Territorial boundaries and matings, 8-14 April 1968. Boundaries indicated by solid lines are based on Facing-past Encounters in Map 8b. The mating center 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 one day Male D defended the western portion of TM's former territory. See Map 5a for explanations of other symbols.

Map 10a. Territorial boundaries, 22-25 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 11a. Territories of individually recognized males (numbers), 8-28 April 1969, Dry Sandy Lek. Boundaries based on records of Facing-past Encounters (see Maps 11b and 11c) 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 50-foot (15.4-meter) grid. Many other males occupied positions in all directions from the mapped area. Males 24, 25, 27, and 28 were yearlings.

- 1 2 3 4
 △ △ Males 20-22, 20-8, 2-12, 6-9, 3-4, 3-19, 6-14, 7-8
 ○ ○ Males 22-13, 8-13, 7-4, 3-6, 4-9, 9-2, 12-21, 9-12, 20-12, 8-9
 □ □ Males 20-13, 9-20, 8-4, 7-19, 6-4, 6-2, 3-11
 8-18 April 1969

Map 11b. Facing-past Encounters, 8-18 April 1969. Numbers identifying each male are placed near the centers 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 50-foot (15.4-meter) grid.

Map 12. Territorial boundaries and matings, 8-28 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 neighbor'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 neighbors 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.

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