THE UNIVERSITY OF MANITOBA

ORGANIZATION AND FUNCTIONS OF THE SPRING AND AUTUMN LEK OF THE SHARP-TAILED GROUSE (*Pedioecetes phasianellus* Linnaeus)

A THESIS

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ABSTRACT

Organization and Functions of the Spring and Autumn Lek of the Sharp-tailed Grouse (Pedioecetes phasianellus Linnaeus).

Robert James Brown

A study of the organization and functions of the spring and autumn lek of the Sharp-tailed Grouse (Pedioecetes phasianellus) was conducted near Hodgson, Manitoba, between the spring of 1968 and the fall of 1969. The objectives of the study were to examine aspects of Sharp-tailed Grouse behavior relating to lek organization, and to gain some insight as to the functional significance of the lek display, particularly its autumn phase.

Ten leks were studied at Hodgson, Manitoba. Six of these leks were large (more than 10 cocks) and four small (less than 10 cocks). Cocks were trapped and banded, then territories were mapped and general observations of lek behavior were recorded during the spring and autumn seasons of 1968 and 1969.

On the basis of the data obtained, it was found that proportionately more adult males tended to be located centrally on the lek, while most juveniles were located more peripherally. For both juveniles and adults, most of the interactions with other grouse on a lek were directed

towards the center of the lek. Territory sizes were variable, those of peripheral birds being greater than those of central birds, and those of birds on small leks being greater than on large leks. Larger territories were also found on leks in tall vegetation compared to those on short vegetation. These results were found to be consistent with an explanation based on the fairly well accepted hypotheses that lek organization is based on an attraction of lek birds to one another, coupled with active defence of territorial boundaries by aggressive behavior, and the existence of a radiating dominance hierarchy.

Several lines of evidence supported the hypothesis that one function of the fall display may be in the dispersion of the species. Movements by individual cocks from small leks to large leks during the autumn display period, shifts of entire leks from one location to another during the fall, and attendance at autumn displays by juvenile males all indicated autumn dispersal. Territory shifts within individual leks also indicated that the fall display may serve as a time when necessary reassortment of territories occurs within the lek itself. The increased vegetative cover on autumn leks, combined with the apparent reduced intensity of the fall lek display, appeared to favor the autumn display period as a time when shifts of leks from one location to another can readily occur.

ACKNOWLEDGMENTS

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INTRODUCTION

A communal display which is characteristic of several species of grouse occurs on an area known as the "lek" (Lumsden, 1965). In North America several English names have been used to describe the display areas of the various lek grouse, for example the "booming-grounds" of the greater Prairie Chicken (Tympanchus cupido) (Hammerstrom, 1939); the "strutting-grounds" of the Sage Grouse (Centrocercus urophasianus) (Simon, 1940); and the "dancing-grounds" of the Sharp-tailed Grouse (Pedioecetes phasianellus) (Amman, 1957). The term "lek" is used here because it is the oldest (Lumsden, 1965), most general, and probably the best known single name.

The lek grouse are only a few of the numerous bird species that use the lek for courtship display and reproduction. For example, the Ruff (Philomachus pugnax), Gould's Manakin (Manacus vitellinus), and the Peacock (Pavo cristatus) (Armstrong, 1947). The possible functions of the lek, and complexity of the behavior patterns involved in the lek display have attracted the interest of a number of investigators in the field of animal behavior and ecology (Table I). A major portion of the present study was to examine a few of the possible functions of the lek and to analyze some of the patterns of lek

TABLE I

Suggested functions of the lek display

	Suggested Functions	Authority
A.	Reproduction	
	1. Place where courtship and copulation occurs	Bent, (1932); Nice, (1941); Schwartz, (1945); Hamerstrom and Hamerstrom, (1955); Ammann, (1957); Evans, (1961); Lumsden, (1965).
	2. Attraction and sexual stimulation of females	Lack, (1939); Hamerstrom and Hamerstrom, (1960); Lumsden, (1965); Robel, (1967).
	3. Synchronization of breeding cycles through social facilitation	Darling, (1938).
	4. Prevention of interference with copulation	Lack, (1939); Schwartz, (1945).
	5. Promotes maximum production through selection of the most vigorous breeding males	Robel, (1967).
B.	Adoption to a sex ratio favoring males	Armstrong, (1947).
C.	Helps disperse species through available habitat	Schwartz, (1945); Wynne-Edwards, (1962); Lumsden, (1965).
D.	Population regulation	Wynne-Edwards, (1962); Robel, (1970).
E.	Protection from predators	Berger et al., (1963); Koivisto, (1965).

organization in the Sharp-tailed Grouse (Pedioecetes phasianellus).

At least nine functions for the lek have been suggested by various workers who have investigated lek phenomena (Table I). Some of these functions, such as a place for courtship and copulation, and attraction and sexual stimulation of hens, have been well documented, but others, such as synchronization of breeding cycles through social facilitation, promoting maximum production through the selection of the most vigorous breeding males, population regulation, and protection from predators, have not received intensive investigation.

Some investigators, including Schwartz (1945), Wynne-Edwards (1962), and Lumsden (1965), have mentioned the possible role of the lek in the dispersion of the species, but these investigators have not subjected this hypothesis to intensive examination, and have based their comments mainly on observations of the location of leks during the spring season. The possibility that the autumn display may be important in the dispersion of the Sharp-tailed Grouse, as it is in at least one non-lek grouse, the Red Grouse, (Lagopus lagopus scoticus) (Watson, 1964), and in several other bird species (Nice, 1941), appears not to have been considered. One purpose of this study was to examine the hypothesis that, as in these other bird species, the autumn

display of the Sharp-tailed Grouse may function in dispersion of the breeding population.

As mentioned above, numerous functions have been suggested for the lek. It seems probable that behavioral characteristics making up the structure and organization of the lek would complement its functions, as is the case in most anatomical structure-function relationships (Griffin and Novick, 1962). Some of these behavioral characteristics relevant to lek organization have been fairly well documented: (Koivisto, 1965) for the Black Grouse, (Lyrurus tetrix), (Scott, 1942) for the Sage Grouse, and (Lumsden, 1965) for the Sharp-tailed Grouse, for example have suggested that there is a radiating hierarchy on grouse leks, with the cocks near the center of the lek tending to be more dominant than those near the periphery of the lek. Organization of the lek in terms of this hierarchy is however, tempered by the fact that each cock regularly attending a lek holds a territory within which he enjoys dominance over his neighbors. Further, the lek appears to be a highly competitive mating system, in that a very small percentage of the displaying cocks ever succeed in fertilizing a hen (Scott, 1950; Peterle, 1954; Evans, 1961; Robel, 1967). It also appears that the number of cocks attending a lek, and the size of the territories and their stability, may vary considerably within a given lek species (Hamerstrom and

Hamerstrom, 1960; Lumsden, 1965). Other aspects of lek structure and organization have received less attention. In particular, little quantitative data exists relating such variables as the number of cocks attending a lek, their position on the lek, or the topography and vegetation of the lek to such characteristics as size and stability of territories. Obtaining quantitative data relating to these variables thus constituted another objective of the present study.

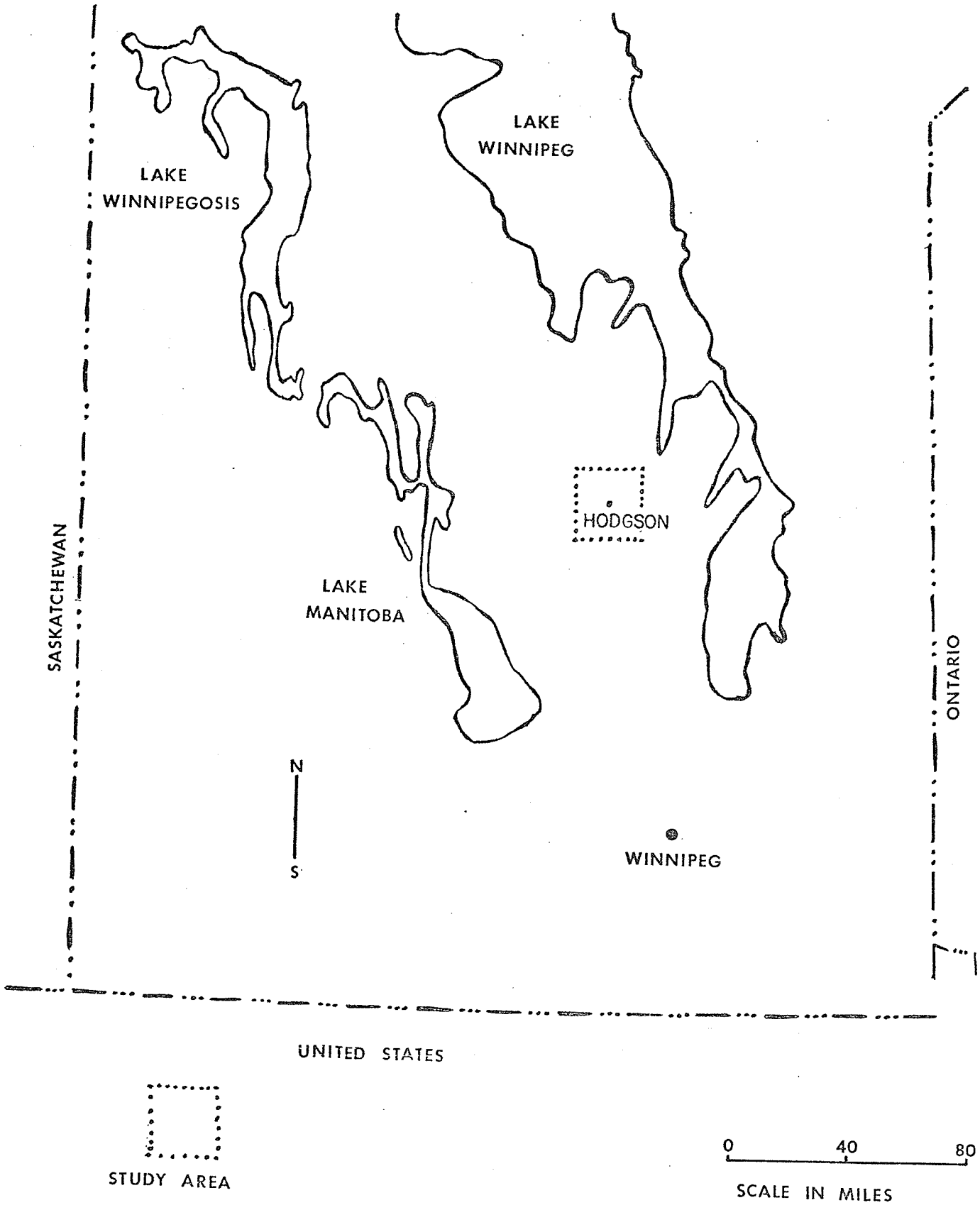
In addition, information was obtained relating to general behavior on the lek, seasonal use of the lek, times of arrivals, time spent on the lek, and lek predation. Observations of the early development of display behavior in young Sharp-tailed Grouse are also included. Four hypotheses of lek formation and maintenance are included as an attempt to conceptualize and integrate the observed behavioral characteristics of the lek grouse with the organizational patterns present on the lek.

STUDY AREA, MATERIALS, AND METHODS

Study Area

The study was located over a 90 sq. mile area lying mainly to the East and North of the town of Hodgson, in the Interlake region of Manitoba, approximately 125 miles north of Winnipeg (Fig. 1). This area is one of transition between the Boreal forests of the North and the Aspen parkland of the South. Topographically, the region consists of low ridges or cuesta, formed from the edges of dipping beds of sedimentary rock (Stearn, 1956). This sedimentary rock is Silurian limestone of the Stonewall formation in the western portion of the area, and Ordivician limestone of the Stony Mountain formation on the eastern portion of the area (Stearn, 1956). The cuestas run predominantly North and South. On the study area they were an average of 4 miles apart, separated by fairly level lowlands. The lowland portion of the study area was in part covered by muskeg or peat and Black Spruce (*Picea mariana*) bogs, but in better drained areas were predominantly grasses such as Reed Bent Grass (*Calamagrostis*) or Bluegrass (*Poa*). While much of the better drained lowlands had been cultivated, the rocky ridges had not. These ridges were either open or covered with a mixture of grasses, shrubs, and broad-leaf or coniferous forests, the proportions of each varying with the soil

Fig. 1. Map of the Province of Manitoba, showing the Hodgson study area.


LAKE
WINNIPEGOSIS
LAKE
WINNIPEG
HODGSON
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UNITED STATES
STUDY AREA
0
40
80
SCALE IN MILES

conditions and the state of plant succession. Samples were taken of the vegetation of the open areas of the ridges, and identified from taxonomic keys (Budd, 1952; Frankton, 1956). They were found to include grasses: Reed Bent Grass (Calamagrostis), Bluegrass (Poa), Junegrass (Koeleria), and Wheat Grass (Agropyron); Herbs: Wild Strawberry (Fragaria), Yarrow (Achillea), Wild Bergamot (Monarda), Asters (Aster), Gentians (Gentiana), Milk vetch (Astragalus), Sweet Clover (Melilotus), and Sage (Artemisia); Shrubs: Wild Raspberry (Rubus pubescens), Cinquefoil (Potentilla), Wild Rose (Rosa acicularis), Bearberry (Arctostaphylos Uva-ursi), Buffaloberry (Shepherdia canadensis), Creeping Juniper (Sabina juniperinus), and Willow (Salix).

The wet meadow vegetation was found to be predominately Reed Bent Grass and Blue Grass.

The vegetation of the forested portions of the study area consisted of shrubs: Willow (Salix), Red Osier (Cornus stolonifera), and Chokecherry (Prunus virginiana), and trees: Oak (Quercus macrocarpa), Birch (Betula papyrifera), Jack Pine (Pinus banksiana), White Spruce (Picea glauca), and species of Populus, of which the Quaking aspen (P. tremuloides) was by far the most abundant. According to a map compiled by E. T. Seton in 1905 (Bird, 1961), the study area was not within the aspen parkland at that time, but was within the boreal forest. Large areas that were once White or Black Spruce have apparently been burned out in the last

50 years (Pers. comm. from A. Thomas, Hodgson, Manitoba) and periodic fires have since kept plant succession at the grass and shrubs stage over a considerable part of the area. The grass and shrublands of the ridges, and the wet meadows of the region create a habitat which supports good populations of Sharp-tailed Grouse.

Locating Leks

Since Sharp-tailed Grouse research had previously been conducted on the study area (Nitchuk, 1969), the locations of 23 leks were known at the start of the study. A search for additional leks was conducted over the study area in 1968 and 1969. Searching for leks was done mainly in early spring, from shortly before sunrise until several hours after sunrise on days which were relatively clear and calm. These are the times when Sharp-tailed Grouse leks are known to be most active (Hamerstrom, 1939).

The procedure consisted of stopping every half mile along the roads in the area and listening for the sounds of the displaying birds. In some areas, walks of up to one mile from the road were also made. Since displaying Sharp-tailed Grouse can be heard for nearly a mile when conditions are clear and calm (Lumsden, 1965), it is probable that this method resulted in the locating of all the active leks over the area searched. Eight new leks were located on the study area during 1968 and 1969. A total of 34 leks were therefore found within the study area. The location of these leks is

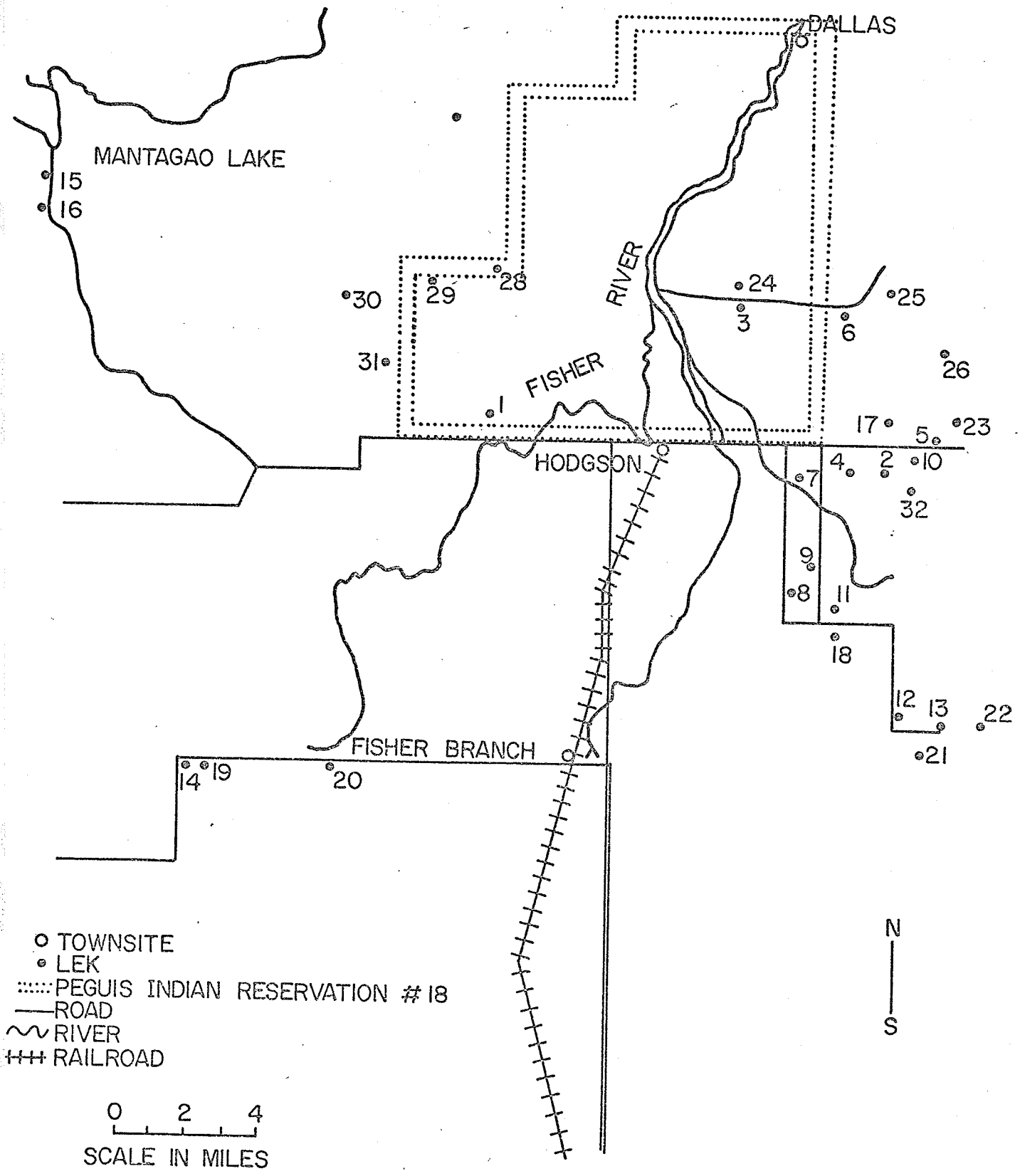
shown in Fig. 2.

In addition to the spring search, an autumn search was also conducted in 1968 and 1969. This consisted mainly of checking previously located leks for signs of activity such as feathers or fresh droppings. A limited version of the spring search was also performed in each autumn. The inconsistency and relatively low intensity of the autumn display considerably lowered the effectiveness of the method at this time.

Trapping

Eighty-five cocks and six hens were trapped on 12 leks during the spring and fall of 1968 and the spring of 1969. The materials used in this trapping program were baited bownets, (Hamerstrom, 1942; Anderson and Hamerstrom, 1967), two 8' x 40' mist nets strung between either three or four 9' aluminum poles; and four cannon nets. All of the successful trapping was done on the dancing-grounds during the morning display period. When bownets were used they were set on the afternoon prior to the trapping morning. This allowed the grouse to habituate to the nets during their evening display, and made it possible to set and bait the traps quickly the next morning. The bownets were placed on known territories, or as near as possible to the center of activity of unknown territories as assessed by feathers and droppings. When possible the bownets were partially

Fig. 2. Map of the Hodgson study area, showing the location and number of all the known Sharp-tailed Grouse leks in the area.


DALLAS
MANTAGAO LAKE
RIVER
FISHER
HODGSON
FISHER BRANCH
15
16
30
29
28
24
25
3
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2
10
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32
9
8
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18
12
13
22
21
14
19
20
TOWNSITE
LEK
PEGUIS INDIAN RESERVATION # 18
ROAD
RIVER
RAILROAD
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covered with light vegetation for camouflage. Bownets were always baited and cocked in the morning, before the grouse arrived. Bait for the bownets consisted of a Sharp-tailed Grouse mounted in the crouching position to resemble a female in the pre-copulatory position (Lumsden, 1965). The mount was placed in the center of the arc made by the set bownet, positioned to face towards the net. When cocks mounted the model the bownet was sprung by a concealed observer. On two occasions two cocks were trapped simultaneously as a result of a second cock rushing in to interfere with the first cock's copulation just as the bownet was sprung. A total of 8 cocks were trapped using this technique, all in the spring of 1968.

In 1968, a movable decoy was used on a small lek containing only 3 cocks in an attempt to lure a cock into the range of the bownet. The movable decoy was made by wiring the previously described bait to a piece of wood, which was nearly concealed by the bait. Using camouflaged fishing line, the decoy could be pulled a distance of 15 ft. along a small groove dug in the ground for this purpose, into the arc of the bownet, after which the head end could be moved up and down approximately 2 inches. On the two occasions that this modification was used it elicited only alarm responses from the nearest cocks, both when it was moved in a straight line and when moved up and down. It is

perhaps interesting that movement associated with the model produced alarm responses, since the same cock copulated with the model on a later occasion when it was not being moved.

On the basis of the limited use made of the bownet in the present study, it appears to be most effective on large dancing-grounds for the purpose of selectively capturing individual birds located towards the center of the lek, without risk of capturing others. The bownet was also used, on one occasion in 1968, to trap a hen on her nest. The hen was first flushed off her nest, and the net was set so that when she returned she would be within range of the bownet. The site was then left, and an hour later I returned, and from a distance of 30' sprung the bownet over the hen.

On small leks, or for capturing birds located on the periphery of large leks, mist nets were found to be more effective than bownets, both in 1968 and 1969. Nets were strung on the evening before the trapping was to occur, and left furled until morning, when they were unfurled before the grouse arrived. On large leks, either a broad "V" configuration or two separate nets were employed, depending on the dispersion of cocks on the lek. The nets were set with their bottom edges 2 ft. off the ground so that the grouse could walk underneath them without becoming entangled. The trappers hid approximately 50 yds. from the lek until the males arrived, then flushed them into the net. On

several occasions mounted grouse in the position of a squatting hen were placed 5 ft. to 15 ft. in front of the nets in an attempt to lure the cocks to the bait area for trapping. It was not possible to determine whether these lures affected the catch significantly.

On small leks (less than 5 birds), due to the large size of the cock's territories, and the tendency of the cocks to wander, the cocks were trapped one at a time. To do this, the extent of the cock's territory was initially estimated by direct observation from a blind. The mist nets were then arranged in a tight "V" over the territory, and a mounted grouse placed at the center of the "V", approximately 20 ft. from the apex. To aid in determining when the cock was in a suitable position in front of the nets so that it would be trapped when it flushed, marking stakes were placed on the territory between the mist nets.

In 1969, mist nets were also used in conjunction with cannon nets on several occasions, as described more fully below. A total of 37 Sharp-tailed Grouse were captured in mist nets in 1968 and 1969. Mist nets were found to be reasonably effective, and inexpensive trapping devices, with extreme portability. Several problems however, were encountered while using them. In order to trap a large proportion of the cocks on a lek it was necessary to use the mist nets on several occasions. This involved

considerable disruption of the lek, and resulted in some birds being captured more than once. Another problem occurred when birds flushed away from the nets as a result of an individual bird flying or flutter-jumping into the mist net before the trappers had flushed the flock. Since most of the other grouse would fly away from the trapped bird, few others would be captured. One other problem associated with the mist nets is that they are indiscriminate in what they trap. During the study, a meadowlark, and an immature Goshawk were accidentally trapped on occasions when the trappers were waiting for Sharp-tailed Grouse. The time involved in freeing these birds jeopardized the trapping program for those days.

During the fall of 1968 and the Spring of 1969, cannon nets were employed as the main trapping device. Three grouse were captured on one occasion during the fall of 1968, when a 60' x 40' cannon net with $1\frac{1}{2}$" sq. mesh was fired, using three cannon of the "Dill" type. In the spring of 1969, 12 cannons of the "Miller" type were obtained.[1] In addition to the net used in the fall of 1968, two 60' x 40' nylon cannon nets of 3" sq. mesh, and one 60' x 40' #189 knotless nylon net[2] with $1\frac{1}{4}$" sq. mesh was used. The charges

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[1] John East Ironworks, Saskatoon, Saskatchewan.

[2] Nicols Net and Twine(R.R.3, Bend Road, East St. Louis, Illinois).

for the Miller cannons were made up in #30F round cardboard pill boxes.[1] An S-121 electric squib[2] was placed in the lower half of the pill-box, with its leads passing through a small slit in the lower half of the box. The powder (Dupont Smokeless 700X Hiskor) was then poured in until the lower half of the box was filled. The lid of the pill box was then put on, and scotch tape was used to seal it. The squibs were wired in series to a 25 amp blasting machine. It was found that three Miller cannons loaded with the charges described can easily pull a 60' x 40' cannon net to full extension.

In trapping with cannon nets the following procedure was used: In cases where the approximate locations of the cocks on the lek were known from observation, the cannon nets were spread out on either side of the area of highest concentration of cocks, in such a way that, when fully extended, they would cover that area and overlap each other by approximately 10 ft. (Fig. 3b). In cases where the approximate territories of the cocks were not known, it was occasionally necessary to spend a morning watching the cocks, during which time, the locations of greatest concentration

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[1]Davis Bros. Inc. (P. O. Box 5027, Terminal Annex, Denver 17, Colorado).

[2]C.I.L. Ltd., 1199 St. James Street, Winnipeg 3, Manitoba.

Fig. 3. Positions of cannon-nets, mist nets, and decoys before (a) and after (b) firing.

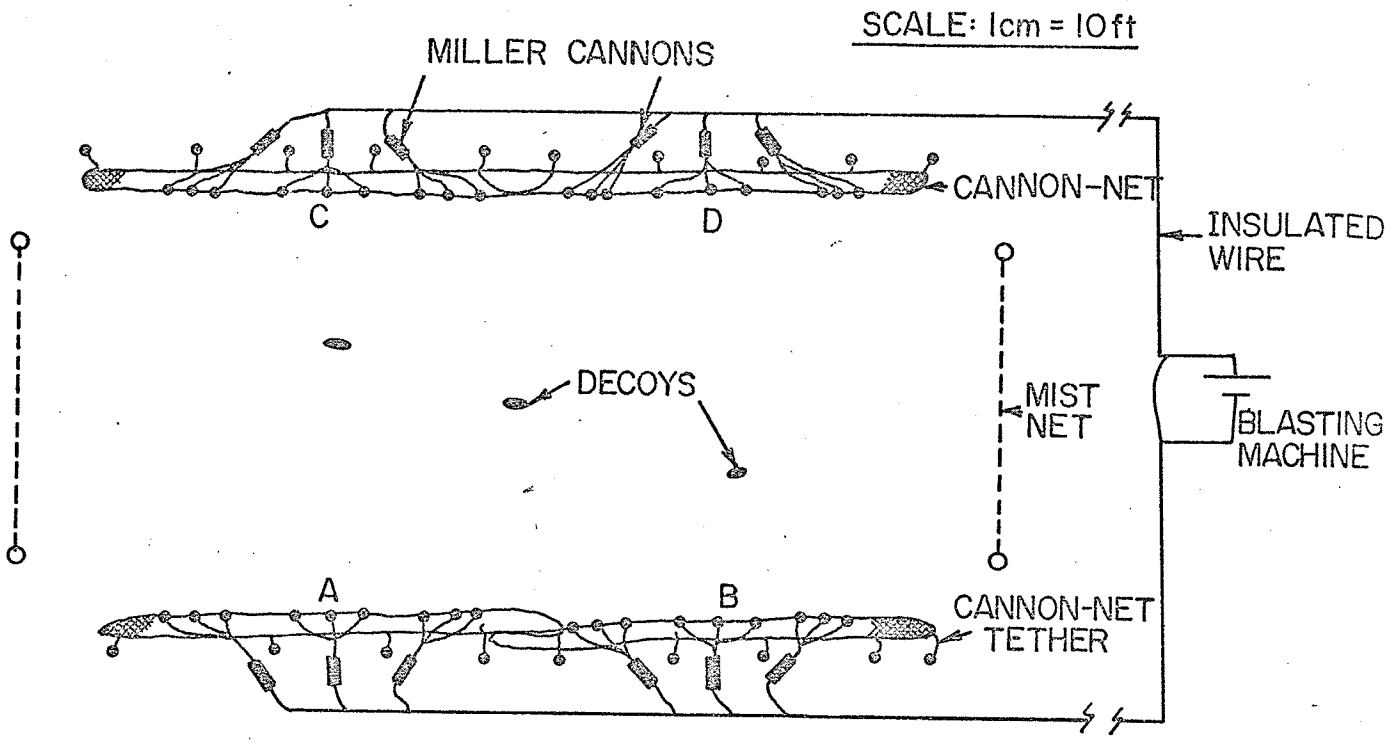

FIGURE 3A

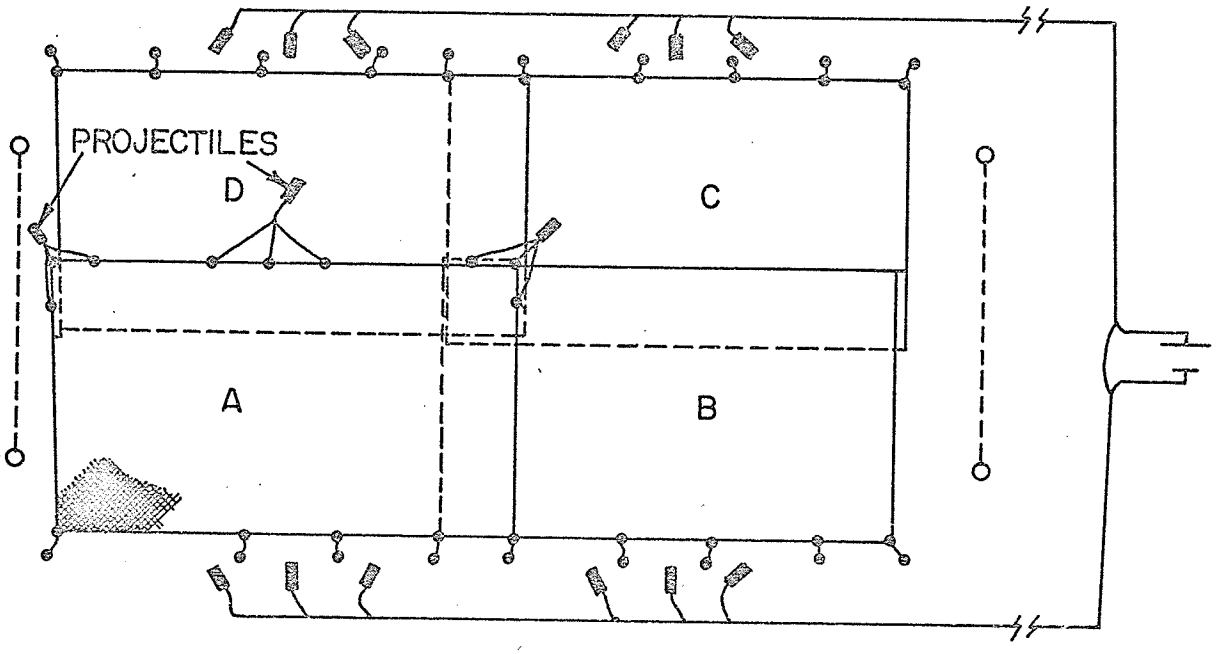

FIGURE 3B

of cocks was ascertained. In several cases, rather than spend a morning watching the display, the lek was examined on the afternoon preceding the trapping. A careful search of the lek was conducted for concentrations of droppings, which were found to be reliable indicators of the locations of grouse. The accuracy of this method was borne out by the fact that trapping success using this method was as great as when territory locations were determined by direct observation. Four nets were then set up in the same way as on leks where the dispersion of the cocks was known (See Fig. 3a). Setting and firing of cannon nets is described by Dill and Thornsberry (1950), and Miller (1957). In the present study nets A and B were both elevated so that they would fire over nets C and D. At the same time, net A was elevated so that it would fire over net B, and net C elevated so that it would fire over net D. In this way, the danger of nets colliding was minimized. On most occasions, two 13m x 2m mist nets were also strung 5m to 7m from the outside edges of the area covered by the cannon nets. Mounts of Sharp-tailed grouse in the form of a crouching hen were used as decoys to attract the cocks to the areas between the nets.

The nets were furled and set for firing on the afternoon preceding the day of firing (Fig. 3). The next morning the trappers entered the blind placed approximately 50m from the lek, waited until the maximum number of birds

appeared to be between the nets, then fired the cannons. The captured grouse were immediately covered with burlap to quiet them, and removed from the nets as quickly as possible. After the grouse were removed from the nets they were held in burlap sacks, while the cannon nets were quickly furled and the mist nets rearranged in such a way that if the untrapped grouse returned while the others were being measured and banded, a second trapping might be made. Using the cannon nets and mist nets, an average of approximately 10 grouse were trapped per morning. Fifty-two grouse were trapped by cannon-nets in the spring of 1969.

Cannon nets have the advantage of trapping most of the cocks on a lek at one firing, thereby reducing lek disruption by repeated trappings, and increasing the time available for gathering data. Out of 54 grouse trapped in cannon nets, 2 suffered serious leg injuries, but otherwise injuries were minor, involving only superficial lacerations around the shoulders in some of the birds that forced their heads through the 3" sq. mesh nets when attempting to fly out. The disruption of the grouse due to cannon-netting a lek in this way is difficult to assess, but no differences were noted between the cannon-netted and mist-netted leks in such things as number of cocks returning after trapping, time elapsed before grouse returned, and size or stability of territories. The fact that untrapped grouse at Hodgson

usually returned to the lek within 20 minutes after firing, and banded cocks usually returned for the evening display on the same day as they were trapped, suggests that the effect of the cannon nets is not too serious, (see also Peterle, 1956). The mist nets, when used with cannon nets, were again some problem, in that on some occasions, cocks became trapped in them, and flushed the others before a proper trapping could be made. The main problem associated with the cannon nets was found to be their bulk and weight, which made their use on remote leks difficult.

Banding

Each grouse captured was marked with a band on each leg and a neck band. Two types of leg bands were used: One, a U.S. Fish and Wildlife Service band, and the other a numbered and colored aluminum leg band.[1] The leg bands were placed on each leg using banding pliers. The color of the band, and the leg on which it was placed were specific for the lek on which the grouse was banded. The leg bands could be seen easily only in early spring, and at no time could the numbers be read unless the bird was killed or captured.

The neck bands were made of plastic fabric,[2] and

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[1]National Band and Tag Co., Newport, Kentucky 41072.

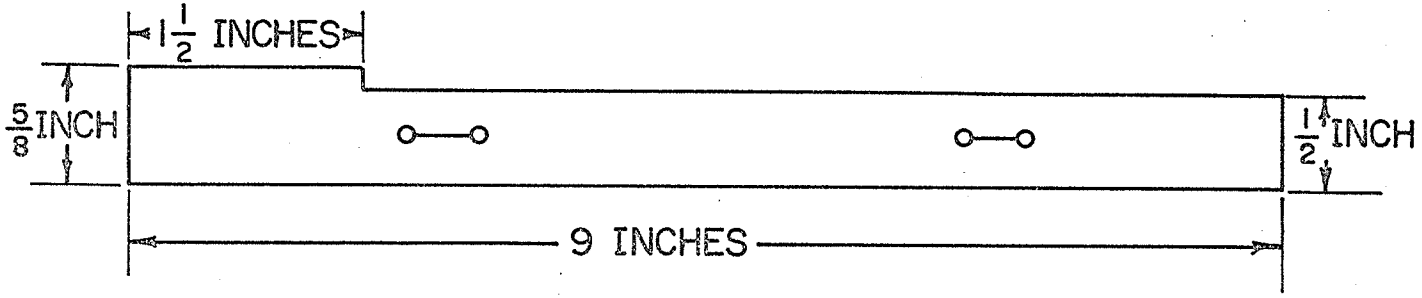
[2]Safety Flag Co. of America, Pine and Conant St., Pawtucket, R.I.

were cut to the approximate dimensions .16cm x 1.3cm x 22.9cm. One end of the band was cut slightly larger than the other. (Fig. 4). This helped to prevent the band from slipping out of the Falconer's Jesse Knot, which was used in placing it around the grouse's neck. The neck bands were either of one piece, or else a piece of different colored plastic was attached to one end by either a steel staple or a copper split-rivet, thus increasing the number of individually identifiable bands. Coding was further increased by cutting the ends of the bands square, pointed, or notched. By recording the colors of the band and the sides of the bird on which the color or cuts were located, each banded grouse could be identified from its neck band at distances up to 400m using 10X binoculars. Some problems were encountered with the neck bands. After being on the birds for several months the ends of some bands tended to curl, thereby making the end cuts difficult to read. The grouse apparently pecked at the neck bands, and the plastic also tended to become brittle in areas where it was covered with feathers. This brittleness may have resulted in some bands falling off.

Age Determination

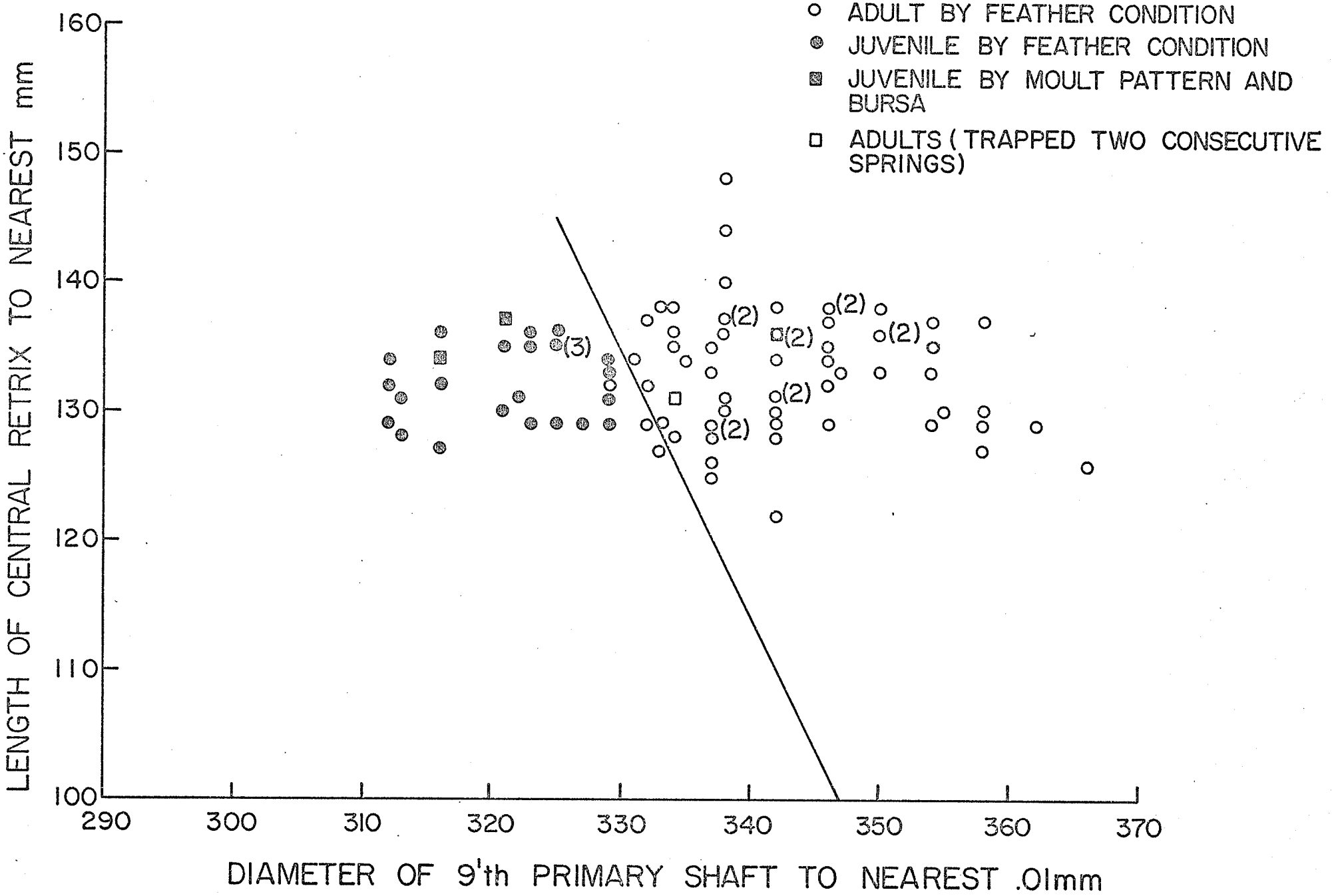
At the time of trapping, each grouse captured was assigned to one of two age classes: juvenile (less than one year of age) or adult (more than one year of age), by examining feather characteristics including color, wear, shape

Fig. 4. Diagram illustrating the shape and size of the neck-bands placed on captured grouse.


1 1/2 INCHES
5/8 INCH
1/2 INCH
9 INCHES

and stage of moult, as described by Ammann (1944) and Wright and Hiatt (1943). The outer two primaries of the juveniles are not moulted in their first year, and thus tend to be more faded and worn than the other primaries. In addition, these two outer juvenile primaries tend to be more pointed than the corresponding primaries in the adult. The length of the central retrix and the diameter of the 9th primary were later measured from removed feather specimens, using calipers and optic micrometer, and the age of the bird again estimated by a scatter diagram (Fig. 5) (Evans, unpublished manuscript; Nitchuk, 1969), on which the adults tend to fall above and to the right of the juveniles. The line used in Figure 5 is based on the one used by Evans (unpublished) on a known aged sample of Sharp-tailed Grouse in Alberta. It is of the same slope, and cuts the abscissa only .02mm from the line used by Nitchuk in aging a sample of Sharp-tailed Grouse at Hodgson in 1969. Evans calculated an error of 5 percent of the aged sample when this line is used as the aging criterion. For this reason, the closest 5 percent of this sample with reference to the line were aged on the basis of feather characteristics alone. When this 5 percent of the sample is ignored, the line shown in Figure 5 is in complete agreement with age determination by retrapping, bursa of Fabricius, and feather condition. Two birds collected in the fall of 1969 were also aged by the

Fig. 5. Scatter diagram showing the plotted values of central retrix length and diameter of the ninth primary for adult and juvenile Sharp-tailed Grouse trapped at Hodgson during 1968 and 1969. In addition, the age determination by retrapping, moult pattern, feather wear, and Bursa of Fabricius are also indicated.


ADULT BY FEATHER CONDITION
JUVENILE BY FEATHER CONDITION
JUVENILE BY MOULT PATTERN AND BURSA
ADULTS (TRAPPED TWO CONSECUTIVE SPRINGS)
LENGTH OF CENTRAL RETRIX TO NEAREST mm
160
150
140
130
120
110
100
290
300
310
320
330
340
350
360
370
DIAMETER OF 9'th PRIMARY SHAFT TO NEAREST .01mm
(3)
(2)
(2)
(2)
(2)
(2)
(2)

bursa of Fabricius (Gower, 1939). Each captured grouse was also weighed using a Chatillon spring scale which was tested with known weights before and after the study and found to be accurate.

Observations

Observations were made from a blind located approximately 5m from the edge of the lek. In 1968, the blind was constructed from burlap and light lumber, but in 1969 a one-piece, sail-cloth blind was used. This blind was more portable than the one made of burlap, and also more opaque. The observer's eye level was 3 ft. 6 in. above ground level, except on two leks where it was approximately 6 ft. Bushnell binoculars and a Bushnell spotting scope with 15X eye piece were used to aid visual observations. A Sony Model TC800 battery operated tape recorder, Uher M514 microphones, Sonocaster 8 ohm, 30 watt loudspeakers and a Fanon transistorized P.A. amplifier model 3512 powered by a 12 volt dry cell were employed when grouse calls were being recorded or played back. Models of Sharp-tailed Grouse mounted in the crouching position were prepared using standard museum specimen procedures and used in some experiments.

To aid in the accurate determination of the birds' positions on the lek, pieces of $\frac{1}{2}$" x 2" lath, painted white, were placed in the ground on each lek at distances of 5 or

10m from each other to form a grid, oriented on North-South axes. The total area covered by the grid was usually 40m square and included most and sometimes all of the lek. By orienting the grid on a North-South axis it was possible to relocate the entire lek, in subsequent seasons, from one permanent reference point. Since many of the leks were located on land which was under cultivation this was an important consideration. The markers were 5m apart on the N - S axis, and 10m apart on the E - W axis. This arrangement was made because the blind was nearly always located either south or north of the lek to prevent the sunrise from blinding the observer, or silhouetting him against the front of the blind. Due to problems of depth perception, it was more difficult to estimate the position of a grouse on the longitudinal axis than on the lateral axis. For this reason, the stakes on a N - S axis were placed 5m apart, and the stakes on the E - W axis were placed 10m apart (Appendix 1). The presence of the grid had little apparent effect on the territorial behavior of the cocks. For instance, movements of the grid had no measurable effect on the location of territories (see p. 87, c.f. Evans, 1969).

The banded grouse attending each lek were observed and their territories recorded during the spring and fall of 1968 and 1969. The territories were recorded by locating the grouse on the lek with reference to the marked grid, and

transcribing its location to an 8 in. x 11 in. piece of paper on which was a scale replica of the lek grid (Appendix 1). Using the markers within ± .5m as determined by actual measurement of test models placed randomly on the lek, the territories of most banded grouse were estimated in this manner on at least two occasions during each season. Additional data, collected for each morning's observations, was recorded on data sheets prepared for this purpose, as illustrated in Appendix II. Daily maximum and minimum temperature readings were obtained from a weather station at Hodgson. General observations of lek behavior were also recorded each day. Mortality on the leks was recorded throughout the study. In addition collections of grouse, sampled on the basis of observed differences in behavior, were made during the fall of 1968 and 1969 for the purpose of documenting the attendance of juveniles and females at the autumn display.

Analyses

Territory measurements were taken from maps drawn to scale as described above. The area of each territory was measured with a planimeter, and the perimeter of each territory measured with a map reader. A center of gravity measure for each territory was obtained by cutting a cardboard outline of the territory and determining its center of gravity with a plumb-line. In all measurements of movement

of territory, the centers of gravity were used as the points of reference. Calculations were made on an Olivetti Underwood Programma 101 calculator. Statistical tests were conducted according to standard procedures described in Cochran (1953), Freund (1960), and Siegel (1956).

In addition to lek observations, such observations as roosting sites, feeding sites, interspecific interactions, nesting sites, behavior of chicks, mortality off the lek, and other miscellaneous observations were recorded throughout the project.

THE AUTUMN DISPLAY

Introduction

In many species of birds there is evidence that autumn displays may function in dispersal of the population, especially the young of the year (Nice, 1941). There is evidence that it may serve a similar function in some grouse species, especially the Red Grouse, in which it has been found (Watson, 1964), that the dispersal of the spring breeding stock is determined by territorial displays during the previous autumn.

Little attention has been given to the possibility that in lek species, autumn displays may have similar functions. Lack (1939) believed the fall display of one lek species, the Black Grouse to be non-functional, and due merely to partial revival of the internal state associated with the spring display, although he has since modified this view (Lack, 1968).

Lek Activity

The autumn display was observed on 18 days in 1968, on 17 days in 1969, and on preliminary occasions in 1967.

Schwartz (1945) and Baker (1953), who studied the Greater Prairie Chicken (Tympanuchus cupido) recorded the earliest autumn lek activity on September 12 and September 15 respectively. Working with Sharp-tailed Grouse in

Alberta, Evans (1961) recorded the earliest fall activity on August 28. The presence of droppings and feathers on most leks in the Hodgson area by the time of earliest examination in the fall (Sept. 12), indicates that the onset of autumn activity in this area occurred in early September or possibly even late August. Once started, lek activity seemed to increase in intensity as the season progressed until an apparent plateau was reached in mid-October, and this level of activity was maintained until mid-November when it declined abruptly, possibly due to the heavy snowfall and low temperatures that occurred at that time. Although the intensity of the display appeared to increase, the time spent on the lek actually decreased as the season progressed (Fig. 6).

In 1969, the arrival times of the cocks changed from before sunrise to after sunrise between October 16 and October 29 (Fig. 7). The dates for 1968 show a similar trend. Hjorth (1968) recorded a similar transition in the Black Grouse of Southern Sweden, however in that case the transition was earlier, occurring during September. As Hjorth suggested for the Black Grouse, it is possible that the change of arrival times from before sunrise to after sunrise (Fig. 7) may be connected with the defoliation of the trees, although definite information of the leaf fall dates for the trees at Hodgson is lacking.

Fig. 6. Time spent on the leks at Hodgson during morning display periods throughout the autumn display periods of 1968 and 1969.

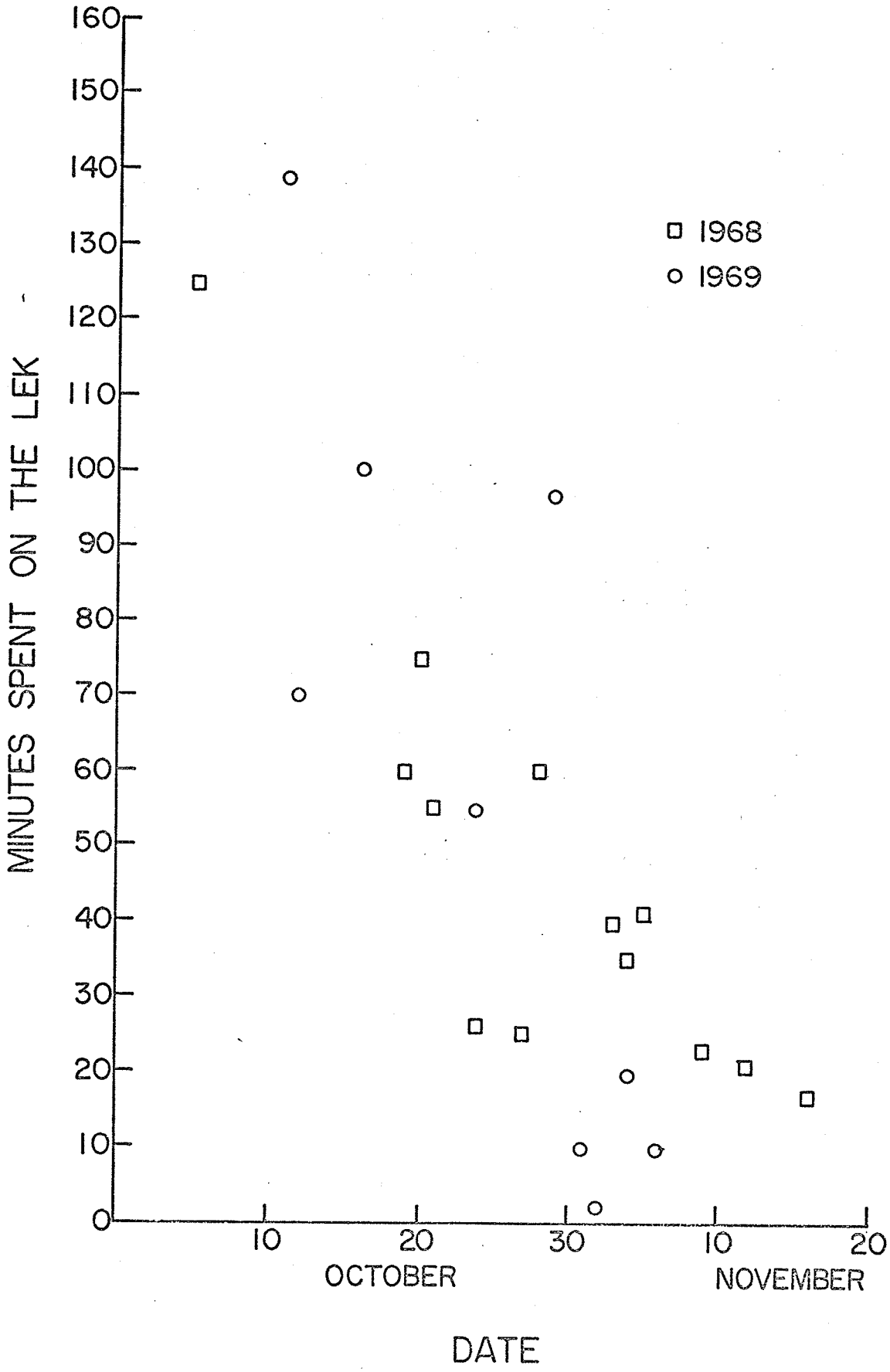
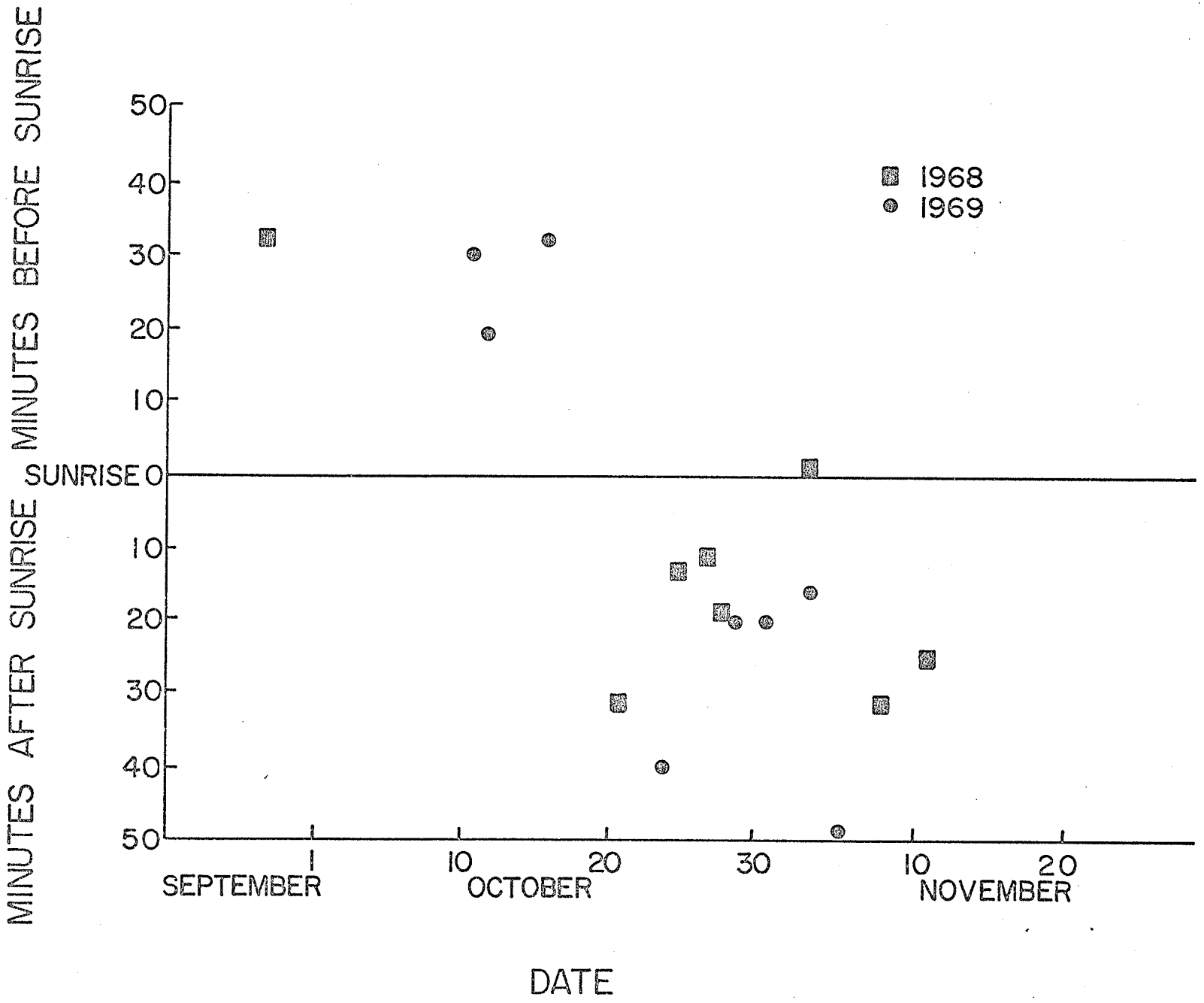

160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
10
0
MINUTES SPENT ON THE LEK
1968
1969
10
20
30
10
20
OCTOBER
NOVEMBER
DATE

Fig. 7. Times of arrival of male Sharp-tailed Grouse on the leks at Hodgson during the autumn display periods of 1968 and 1969 expressed as minutes before or after sunrise.


MINUTES AFTER SUNRISE MINUTES BEFORE SUNRISE
50
40
30
20
10
SUNRISE 0
10
20
30
40
50
1968
1969
SEPTEMBER
1
10
20
OCTOBER
30
10
20
NOVEMBER
DATE

The Autumn Display Compared to the Spring Display

Autumn lek activity was low compared to the spring display. This lower level of activity was reflected in several aspects of the display. Thus, cocks arrived later (Fig. 7), and spent less time on the lek (Fig. 6) during fall than they did during the spring display. These differences were tested by the Median Sign Test and Chi Square, or Fisher Exact Probability Test and found to be significant beyond the .005 level of significance for the 64 arrival times measured, and significant at or beyond the .025 level of significance for the 52 records of time spent on the lek. It was also evident that the general intensity of the display was lower in the autumn than in spring, as was found for the Greater Prairie Chicken by Schwartz (1945). Although no quantitative indices of activity were used such as those of Robel (1965), reduced activity in the autumn was indicated by less movement on the lek, and the virtual absence of such high intensity sounds as the "bottle pop" or "chilk" calls (Lumsden, 1965), which are common in the spring. In addition, as was found for the Black Grouse (Lack, 1939), mounted models of grouse in the attitude of a receptive hen, which in spring elicited courtship and copulation, failed to elicit any such response during the autumn display.

The Autumn Display and Dispersal

During the present study data were collected to

assess the hypothesis that fall displays in Sharp-tailed Grouse may be important in population dispersion.

Dispersal between Leks: During two autumn display periods three marked grouse moved from one lek to another (Table II). One of these moves occurred in the fall of 1968, and one in the fall of 1969. The third move began in the very late spring (June 16) of 1969, and was consolidated in the fall of 1969. The move made in the fall of 1969 from a small lek (#10) to a large one (#2a) remained stable on lek #2a during the spring of 1970. No other moves between leks were observed in the autumn, and none were noted between autumn and spring. It is perhaps significant that all these moves were from small leks that had no birds on them in the autumn, to larger, active leks. Schwartz (1945) found that leks that were inactive in the fall were again active the following spring, but he had no data to indicate where or whether the cocks from the inactive leks displayed in the autumn. At Hodgson two of the individuals moving were able to obtain a central territory on the lek to which they moved.

In addition to moves by individual birds from one lek to another, four instances were recorded in which the entire lek shifted location. All four of these shifts occurred in the fall (Table III). Two leks shifted during the autumn of 1968, and remained stable on their new

TABLE II

Summary of inter-lek movements by individual cocks at Hodgson during 1968 and 1969

Cock#	Original lek#	New lek#	Distance moved	Date of move
110	10	2a	800m	Fall 1968
184	5	23	600m	Late spring and fall 1969
186	35	2a	600m	Fall 1969

TABLE III

Lek movements observed at Hodgson during the autumn display periods of 1968 and 1969

Lek#	Old site	New site	Distance of move	Date of move
2	ridge overgrowing with rose, raspberry, etc.	open meadow with mowed grass	200m	Fall 1968
14	open, shortly cropped grass in heavily grazed pasture	open meadow, grass 6 inches tall	600m	Fall 1968
31	level, open, alfalfa	ploughed (old lek site ploughed as well)	200m	Fall 1969
33	open, slightly elevated, on ploughed field	another part of the ploughed field	100m	Fall 1969

locations in the spring of 1969. One of these moves was from a ridge which was becoming overgrown with tall vegetation, to an adjoining open meadow of mown grass, a distance of approximately 200m away. The other two lek shifts occurred in the fall of 1969, and were fairly short moves (100m and 200m). Both these moves occurred on freshly ploughed fields, and could not be related to any change on the old site of the lek. These moves may have been due to a lack of landmarks by which the grouse could find the old site. The fact that the grouse are able to return to their old lek locations when it is covered with a considerable amount of snow (Anderson, 1969; see p. 88), tends to put this interpretation in question.

Ammann (1957) also recorded a similar instance of a lek shifting in September and remaining stable in its new location for several years. These findings are also consistent with those of Hamerstrom and Hamerstrom (1951), who expressed the suspicion that Sharp-tailed Grouse leks are sometimes established in the fall, and Schwartz (1945) who suggested that Prairie Chicken booming-grounds shifted location in the fall as well as in the spring. Others have recorded lek movements in the spring (Anderson, 1969; Nitchuk, 1969), but the fact that they can occur in the fall, and tend to remain stable thereafter would suggest that autumn displays do, on some occasions, serve as

mechanisms by which populations redistribute themselves in their habitat.

Autumn Recruitment: All active leks censused showed recruitment in the fall, and in at least two instances there were many new birds, which in some cases amounted to as many as the spring complement of the lek (Table IV) (Fig. 8). Lumsden (1965) recorded a similar increase in numbers on the autumn leks. As described above, it was found that at least some of these recruits were cocks which had shifted from small to large leks in the fall. Juveniles were also found to contribute to autumn recruitment. Four males classed as juveniles on the basis of bursa of Fabricius and feather and moult condition (see Methods), were collected on three different leks during the fall display periods of 1968 and 1969. One additional bird, trapped on an autumn lek, was found to be a juvenile on the basis of feather and moult conditions. The sex of the collected specimens was established by dissection of the testes. The sex of the bird trapped on the fall lek was established by retrix patterns (Henderson et al., 1967) and Crown Feathers (Snyder, 1935). The fact that this individual displayed as a cock the next spring confirmed this identification.

Recruitment was found to be significantly higher ($P \leq .02$ Median Sign Test and Chi Square Test) on leks that moved than it was on leks that didn't. Recruitment to leks

Fig. 8. Numbers of male Sharp-tailed Grouse on 7 leks at Hodgson during the spring and autumn display periods of 1968 and 1969. Shaded portions represent #recruits (i.e. birds that did not attend during the spring). S = spring census, A = autumn census, X = no cocks attending the lek during the season.

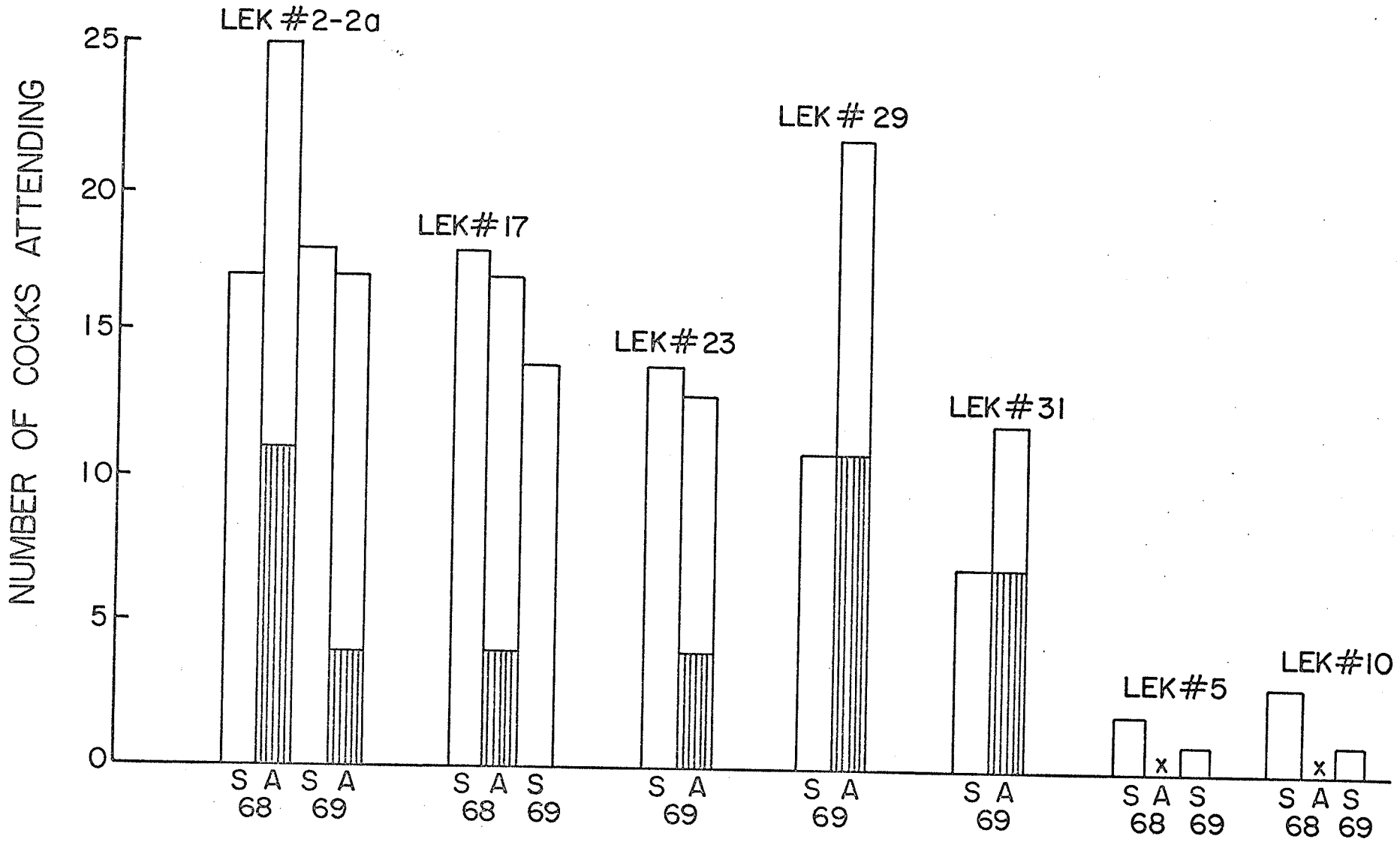

NUMBER OF COCKS ATTENDING
25
20
15
10
5
0
LEK #2-2a
LEK#17
LEK#23
LEK # 29
LEK #31
LEK#5
LEK#10
x
x
S A S A
68 69
S A S
68 69
S A
69
S A
69
S A
69
S A S
68 69
S A S
68 69

TABLE IV

Changes in the numbers of male Sharp-tailed Grouse attending 11 leks at Hodgson between the spring and fall seasons of 1968 and 1969

Lek#	Spring 1968	Fall 1968	Spring 1969	Fall 1969	Known losses from Spr./68 to Fall/68	Recruitment Spr./68 to Fall/68	Known losses from Spr./69 to Fall/69	Recruitment Spr./69 to Fall/69
2,2a*	16	25	18	17	2	11***	5	4
5	2	+**	1	+	--	--	--	--
10	3	+	1	+	--	--	--	--
17	18	17	14	+	5	4	--	--
23	12	--	14	13	--	--	5	4
31	Not observed in 1968		11	22	Not observed in 1968		2	11***
32	"		13	+	"		--	--
33	"		7	12	"		--	7***
34	"		16	+	"		--	--
35	"		5	+	"		--	--

*The grouse from lek #2 moved 200m to a new location in Fall 1968, the new lek is designated #2a.

**The symbol "+" indicates that the lek was inactive.

***Indicates recruitment on leks that moved.

that moved in the fall totalled 29 out of 55 cocks, while recruitment on leks that remained stable in the fall totalled 16 out of 50 cocks.

Lumsden (1965) and Schwartz (1945) have both reported that female as well as male Sharp-tailed Grouse are present on the fall leks. No evidence for female attendance in the fall was obtained from the present study at Hodgson.

The above results document recruitment to the leks during the autumn, and also show that the recruits consist at least in part of juvenile males, and adult males from other leks. It remains possible that females made up some of this recruitment (Lumsden, 1965; Schwartz, 1945). Robel (1969) has suggested further that in Black Grouse, a portion of the male population in spring do not attend leks. If this is also true for Sharp-tailed Grouse, then possibly some of the autumn recruitment to the leks of Hodgson may have consisted of previously non-territorial males, but proof is lacking. The evidence that was obtained, however, is consistent with the hypothesis that the autumn lek is involved in dispersion of at least a portion of the population, including both young and adult males.

Redistribution within Autumn Leks: In addition to effecting the dispersion of the grouse on their habitat, the presence of juvenile males, or strange adult males, at the fall lek may cause redistribution of the cocks within the

lek itself. Some direct evidence of such reassortment was obtained. Out of 18 cocks whose territories were measured from spring to fall, 8 changed position, going from peripheral locations to central locations on the lek or vice versa. Of these changes, six were from peripheral to central, and two were from central to peripheral. The increase in numbers attending the lek may have been responsible for some previously peripheral birds becoming central merely by holding their previous territory against encroachment by the newcomers. Evans (1969), also found some evidence for such territorial rearrangement during the fall.

In addition to the above results that indicate some shift, and hence dispersion during the fall display, there was, as expected, a rather high degree of stability on many leks between seasons (see Appendix III). For example, of 29 color-marked males observed in both spring and fall all but three displayed with the same group in both seasons. Further, of 12 leks studied, only four showed any significant shift in location. Two of these four shifts may have been due to a lack of landmarks, since they were of short distances (100m, 200m), and occurred within ploughed fields.

These latter results, far from being contradictory to the dispersion hypothesis, are rather entirely consistent with it, in that they indicate that the autumn display tends

to localize many male Sharp-tailed Grouse, making them "resident" in somewhat the same sense that some Song Sparrows (Melospiza melodia euphoria) (Nice, 1941), or Red Grouse (Lagopus lagopus) (Watson, 1964), become resident after the fall display period, while simultaneously providing a mechanism by which other males may redistribute themselves with reference to these "residents."

Relationship to Vegetative Cover

Anderson (1969) found that increasing cover height caused booming Prairie Chicken to shift lek locations during the spring season. Schwartz (1945) found that in both seasons the amount and height of cover influence the location of the leks of booming Prairie Chickens, and also noted that those leks not used in fall bore considerably higher vegetation than those leks which were used in the fall. At Hodgson, similar results were found, in that all the leks which were active in the fall were on short vegetation, and in one case, a lek clearly moved from a region of heavier vegetation to an open, short-grass location.

Discussion

In at least some avian species it is known that both adults and juveniles may establish territories in fall which remain more or less stable through to the following spring, for example the Red Grouse (Watson, 1964), and the Song

Sparrow (Nice, 1941). In Sharp-tailed Grouse there is also evidence that at least some adult birds may hold essentially the same territory in spring as they did the previous fall (Evans, 1969) (Appendix III). This evidence, coupled with the other data gathered here, does tend to support the hypothesis that the fall display may function in dispersal. That aspect of the autumn display thus seems to be consistent with what is known for the Red Grouse and many other birds. The evidence also seems consistent with the view that reduced display intensity in the fall, coupled with maximum vegetational effects in the fall, might represent a major mechanism tending to facilitate this fall dispersion.

BEHAVIOR ON THE LEK

Introduction

The greatest lek activity occurs during the breeding season, which extends from early spring to early summer. In the northern portion of the United States and in Canada, the period of regular lek activity by the cocks generally extends from late March until mid-June (Hamerstrom, 1939; Ammann, 1957; Evans, 1961). It is predominantly during the peak of this period (approximately the last week in April and the first week in May) that the females attend the leks and are fertilized there. Lek grouse in more southerly latitudes, where spring and summer arrive considerably earlier, show correspondingly earlier dates for commencement of regular lek activity and peak attendance by hens (Lehmann, 1941; Schwartz, 1945; Baker, 1953). In Attwater's Prairie Chicken (Tympanuchus cupido attwateri), a subspecies native to the Texas gulf coast, lek activity commences in late January or early February, peak hen attendance occurs by early March, and lek activity ends in late May (Lehmann, 1941).

The spring breeding behavior has been described for several of the lek grouse: the displays of the Black Grouse (Lack, 1939; Hohn, 1953; Koivisto, 1965; Kruijt and Hogan, 1967; Hjorth, 1966, 1968), the Sage Grouse (Centrocercus urophasianus) (Simon, 1940; Scott, 1942; Eng, 1961, 1963;

Lumsden, 1968), the Greater Prairie Chicken (Breckenridge, 1929; Hamerstrom, 1939; Schwartz, 1945), and the Sharp-tailed Grouse (Hamerstrom, 1939; Ammann, 1957; Evans, 1961; Lumsden, 1965) have all been dealt with in some detail. The descriptive names of the various displays which will be mentioned in the following discussion are taken from Lumsden (1965).

Lek Attendance by Males

Although the heaviest and most regular attendance occurs during the spring and, to a somewhat lesser extent, the fall seasons, the males of most northern lek grouse also attend the lek periodically throughout the winter when weather conditions are favorable (Hamerstrom, 1939; Ammann, 1957; Peterle, 1954; Koivisto, 1965). At Hodgson the earliest observations, made on March 7, 1969, revealed some indications of recent activity on the two leks examined at that time despite the presence of between one and three feet of snow. These indications of lek activity consisted of markings in the snow which could only have been made by a tail-rattling Sharp-tailed Grouse, and a number of grouse droppings and feathers.

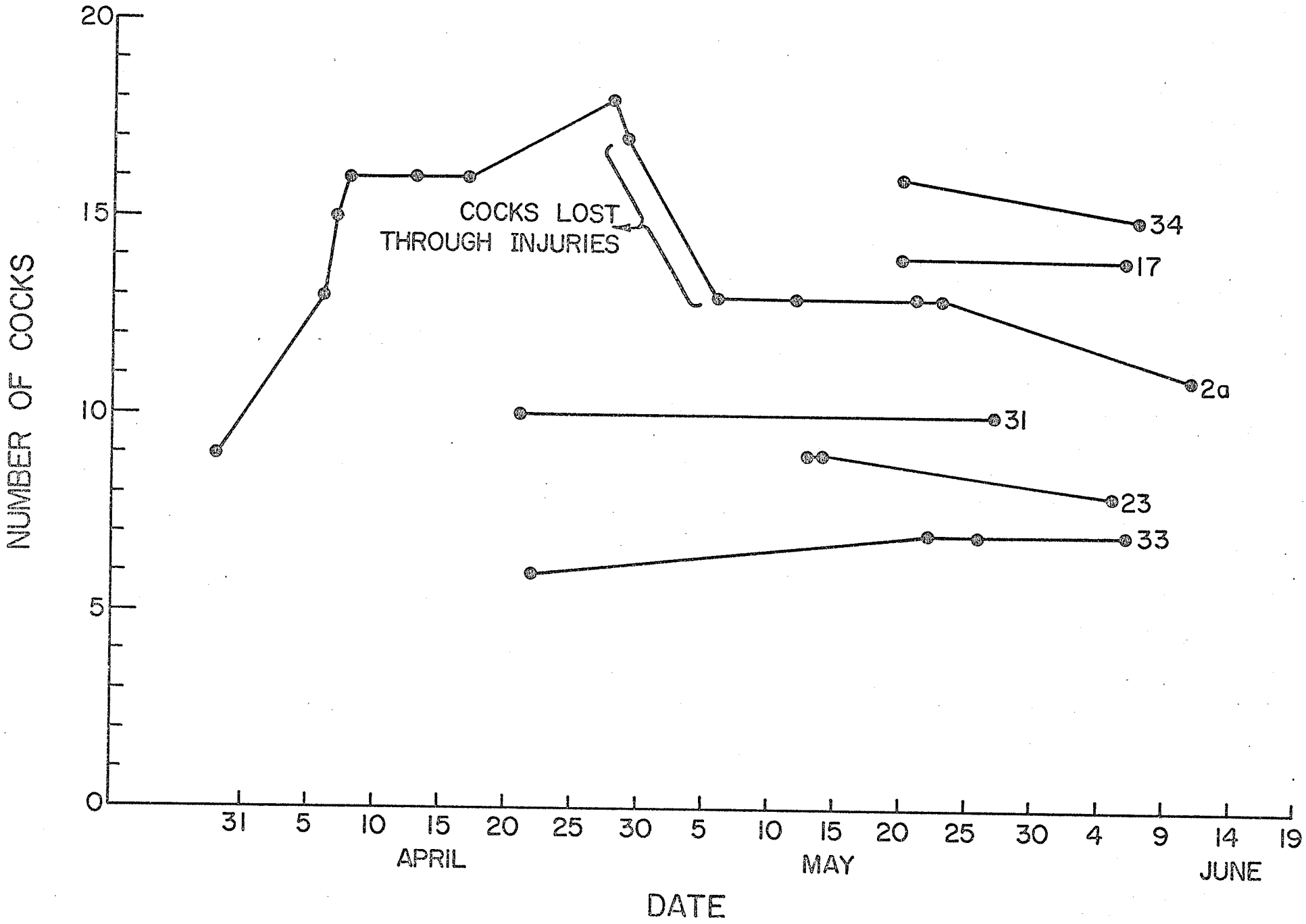
Several of the droppings observed on the leks in early March were of a relatively large size (3" x 1" x 1"), and of a runny consistency. This type of dropping was found on the leks until the first week of April, but not after

that. It may be that these droppings are a result of a change in diet from buds and catkins, and such fruit as rose hips, to lower growing fruits and greens which is known to occur in the early spring (Grange, 1948).

By the end of March, the cocks were attending the leks at Hodgson every morning. On March 29 and 31, 10 grouse were observed actively displaying on lek #2a despite temperatures of -25°C and -23°C respectively. It was, however, clear and calm on both days.

The number of cocks attending lek #2a increased as the season progressed, with a maximum number being recorded during the last week of April, at the approximate peak of spring lek activity (Fig. 9). It might be noted here that despite the increase in attendance between the beginning of April and the end of April, at least one cock (#120) which had attended on April 17 was not present at the peak of lek activity two or three weeks later, thereby indicating even more recruitment to the lek during that period than is indicated in Figure 9. After the peak of activity the number of cocks attending the leks remained relatively stable except immediately after banding which, as discussed below, sometimes caused a decrease in numbers attending. A slight decrease in attendance was noted on several leks toward the end of the reproductive season (Fig. 9). A similar decrease in attendance toward the end of the spring was noted by

Fig. 9. Maximum daily numbers of male Sharp-tailed Grouse attending 6 leks at Hodgson during the spring season of 1969 - lek number is indicated at the right of each polygon.


NUMBER OF COCKS
20
15
10
5
0
COCKS LOST
THROUGH INJURIES
34
17
2a
31
23
33
31
5
10
15
20
25
30
5
10
15
20
25
30
4
9
14
19
APRIL
MAY
JUNE
DATE

Evans (1961). The latest recorded attendance of cocks on the leks at Hodgson was on June 19 in 1968. By mid-June in both 1968 and 1969 lek activity had decreased to the point where attendance was occasional rather than regular, with even the larger leks being sometimes completely inactive on clear mornings.

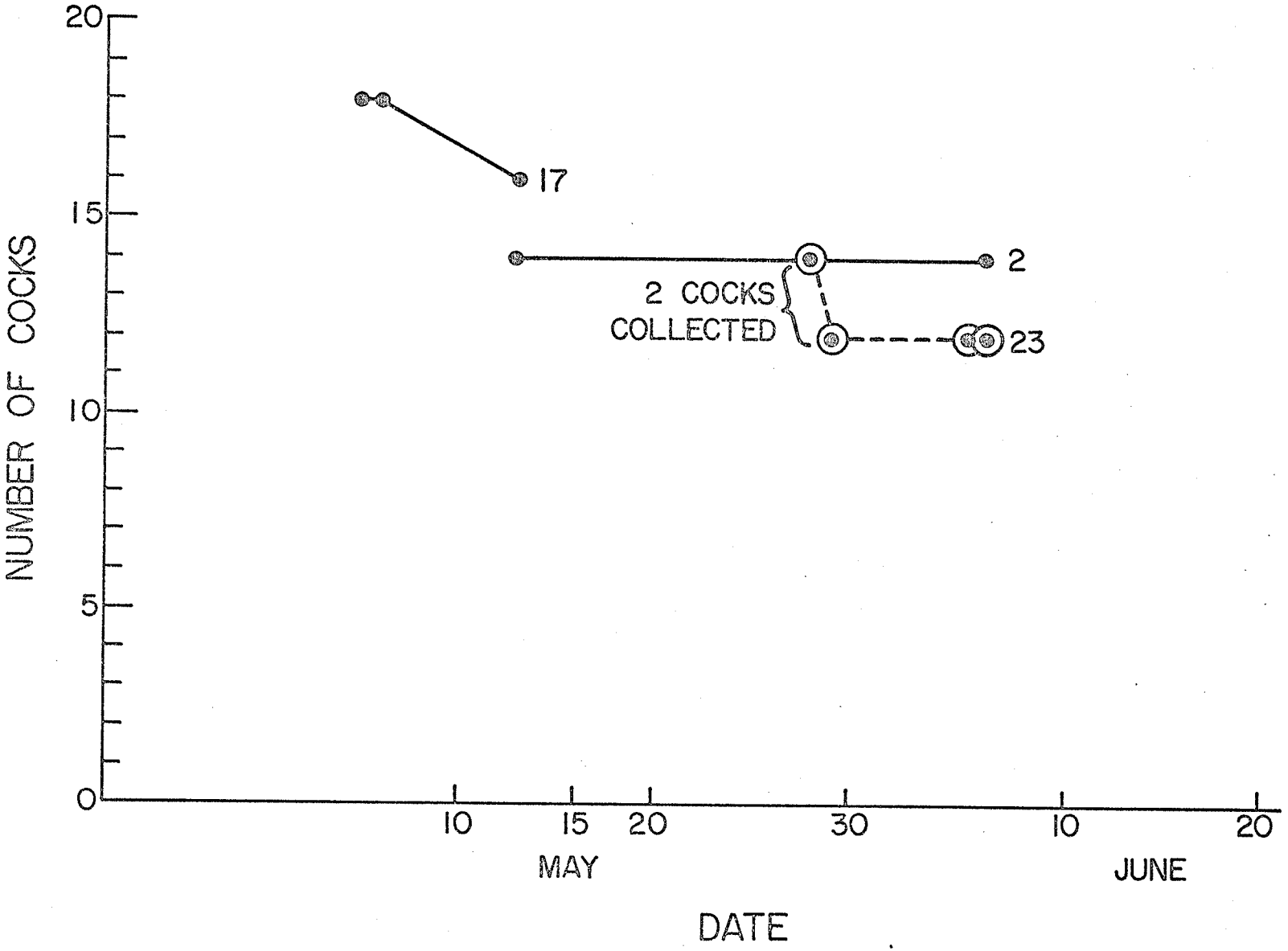
Although no quantitative data were gathered on display intensity it was evident that the intensity of activity on the leks increased during early April, reached a peak near the end of April, when the maximum number of hens were attending, and then fell off steadily until lek attendance stopped in late June. By the beginning of June, active display tended to be restricted to a short period after the cocks arrived each morning, or when a hen attended the lek; the remainder of the time being spent in the various quiescent types of lek behavior which are described in Lumsden (1965).

On 3 of the 5 leks censused before banding operations were carried out, the number of cocks attending was reduced by an average of 17% immediately after banding, and in all three instances attendance never returned to its original level. This was noted for both mist-netted and cannon-netted leks. Lek #2a for example, which was censused both before and after banding operations, showed a decrease of 4 cocks, three of which were banded birds. One of these

three lost a leg during trapping and was not expected to return. Another of these three was killed on the lek, possibly by a predator (see p.107), between the time of trapping and the first observation morning 7 days after trapping. The fate of the other two cocks that did not return was not determined. The banded cock (#161) was not seen on this lek or any other in the fall of 1968 or spring of 1969 however, and therefore may have been killed. Leks #31 and #33 (Fig. 9) were also censused before and after banding. These leks, in contrast to lek #2a, showed a 100% return of banded cocks within 36 and 27 days respectively after banding, and did not show any decrease in attendance, until at least late May (#31) or early June (#33). Reductions in lek attendance not due to recent banding operations are also illustrated by the graphs for leks #34 and #23 (Fig. 9), which represent attendance from two weeks after banding operations were conducted on them on April 30 and April 23 respectively, until early June. The lek attendance data for 1968 is relatively meager, but two leks censused both in May and on into June, showed no decrease in attendance. Both of these leks had cocks removed from them during the season (leks #2, #23; Fig. 10). The decrease observed on lek #17 may have been due to banding operations which immediately preceded the drop in attendance (Fig. 10).

Evening attendance was often lower than in the

Fig. 10. Maximum daily numbers of male Sharp-tailed Grouse attending 3 leks at Hodgson during the spring season of 1968 - lek number is indicated at the right of each polygon.


20
15
10
5
0
NUMBER OF COCKS
17
2
2 COCKS
COLLECTED
23
10
15
20
30
10
20
MAY
JUNE
DATE

morning (Table V). Out of 20 occasions where evening attendance was recorded, 10 showed lower attendance than the typical morning census. For the same leks the evening attendance was never greater than in the morning of the same day. The difference in lek attachment between morning and evening displays presumably results in some segregation of the lek cocks into two or more groups for at least part of the day, a phenomena apparently not considered by previous workers. The significance of this segregation, and the extent to which these groups reunite, if at all, prior to roosting for the evening, was not determined.

Lek Attendance by Females

The attendance of hens on lek #2a during the spring of 1969 is listed in Table V and illustrated as a percentage of male attendance by the bars in Fig. 11. The first attendance of hens on lek #2a in 1969, was recorded on April 13. As indicated by the value for April 28, 1969, in Fig. 11, the peak of hen attendance at Hodgson probably occurred during the last week of April, and coincided with the peak of male attendance as indicated in Figure 9 and Table V. The last observation of hens on lek #2a occurred on May 23 in 1969. The latest observation of a hen on any lek (#33 containing a maximum of 7 cocks), was on June 11, 1969. Attendance by females on seven leks during 1968 and 1969 is summarized in Table V and Figure 11.

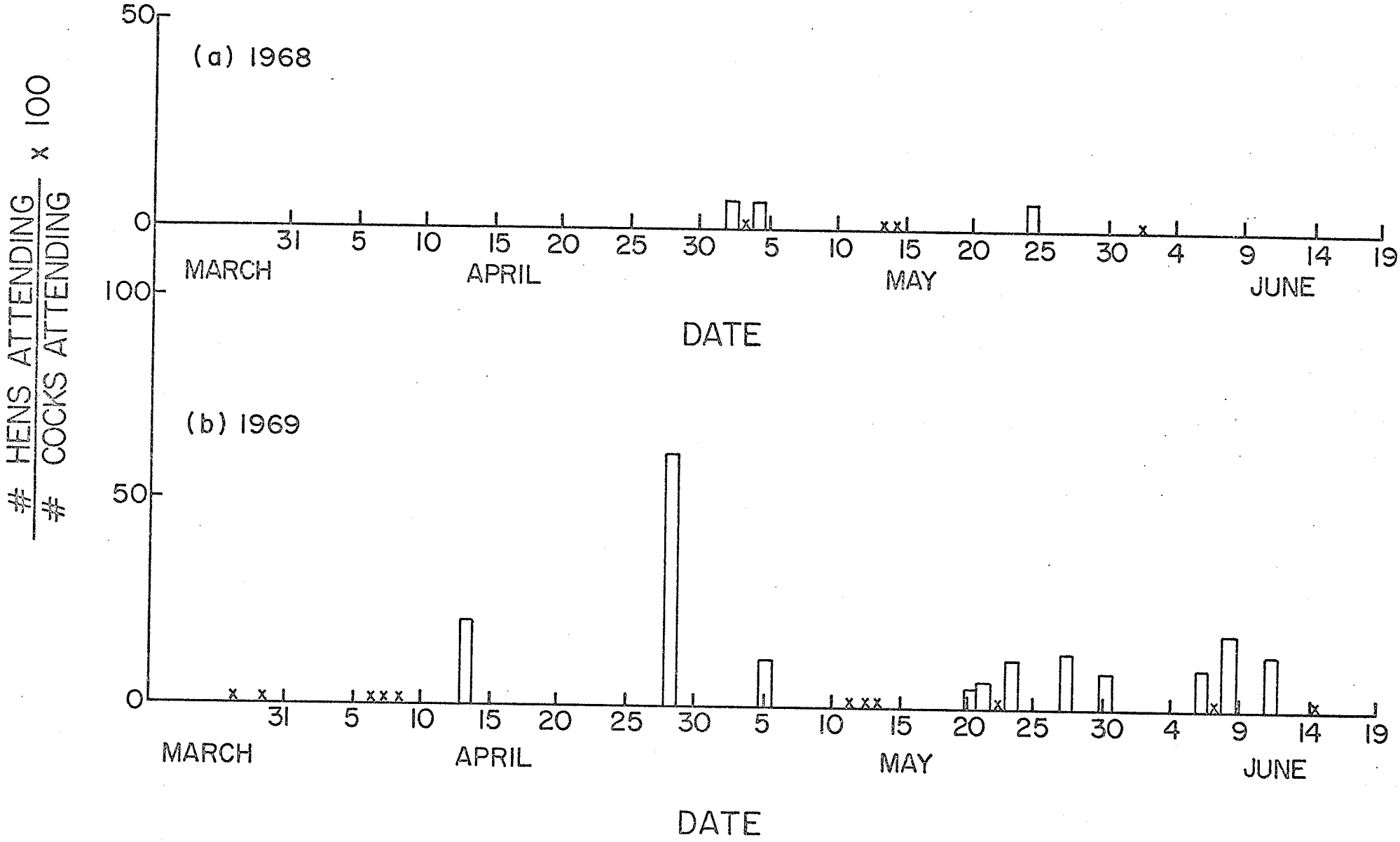
TABLE V

Maximum numbers of male and female Sharp-tailed Grouse on 11 leks at Hodgson during the morning and evening display periods. Spring seasons, 1968 and 1969

1968				1969							
Lek#	Date	#cocks	#hens	Lek#	Date	#cocks	#hens	Lek#	Date	#cocks	#hens
2	May 13	12	0	2a	Mar.29	9	0	31	Apr.21	10	0
	13	12*	0*		31	10	0		May 26	8*	0*
	June 6	12	0		Apr. 6	13	0		27	10	0
17	May 3	17	1		7	15	0	32	May 27	10*	0*
	4	18	0		8	16	0		29	10	1
	4	7*	0*		13	16	3	33	Apr.21	6	0
	5	7*	0*		28	18	11		21	6*	0*
	7	8*	0*		29	17	9		May 23	7	0
	8	18*	0*		May 6	13	2		26	7	1
	13	14*	0*		7	5*	0*		Jne.11	7	1
	14	12	0		8	1*	0*	34	May 19	11*	0*
7	May 10	7	0		12	13	0		20	16	1
	15	7*	2*		12	9*	0*		June 6	10*	0*
23	May 28	12	0		21	13	0		7	15	3
	28	12*	0*		23	13	2	35	May 8	7	0
	29	10	0		Jne.13	11	0		8	7*	0*
	30	10	0	17	May 11	9*	0*				
	June 5	10	0		21	14	1				
	6	10	0		June 6	14	0				
4	May 28	17*	3*	27	May 5	10*	0*				
	29	15	0		13	10	0				
					14	10	0				
					June 5	7	1				

*Counted in afternoon or evening.

Fig. 11. Daily attendance of hens on leks at Hodgson during the spring season of 1968 (a) and 1969 (b), expressed as a percentage of the number of cocks that regularly attended the lek on which the hens were observed. X = days when no hens were observed on the lek.


50
(a) 1968
0
100
31 5 10 15 20 25 30 5 10 15 20 25 30 4 9 14 19
MARCH
APRIL
MAY
JUNE
DATE
(b) 1969
50
0
31 5 10 15 20 25 30 5 10 15 20 25 30 4 9 14 19
MARCH
APRIL
MAY
JUNE
DATE
HENS ATTENDING / # COCKS ATTENDING x 100

When cannon nets were fired over the leks to trap males for banding purposes, attending females were inadvertently trapped on 4 different leks during the peak of lek activity. Between April 21 and May 2, 1969, of 7 hens which were trapped during this period 6 were considered to be adults (two or more years old) whereas only one was classed as a juvenile. If the probability of trapping an adult does not differ significantly from that of trapping a juvenile, the probability of trapping by chance 7 adults and 1 juvenile would be only 0.055 as calculated by the binomial distribution. Since the actual number of juvenile females in a stable population is probably at least equal to the number of adult females (Ammann, 1957), this probability may represent a maximum value. This sample is small, but the ratio of seven adult to one juvenile female in my sample, suggests that further investigation might profitably be made into the possibility of differential lek attendance and hence mating success between adult and juvenile females.

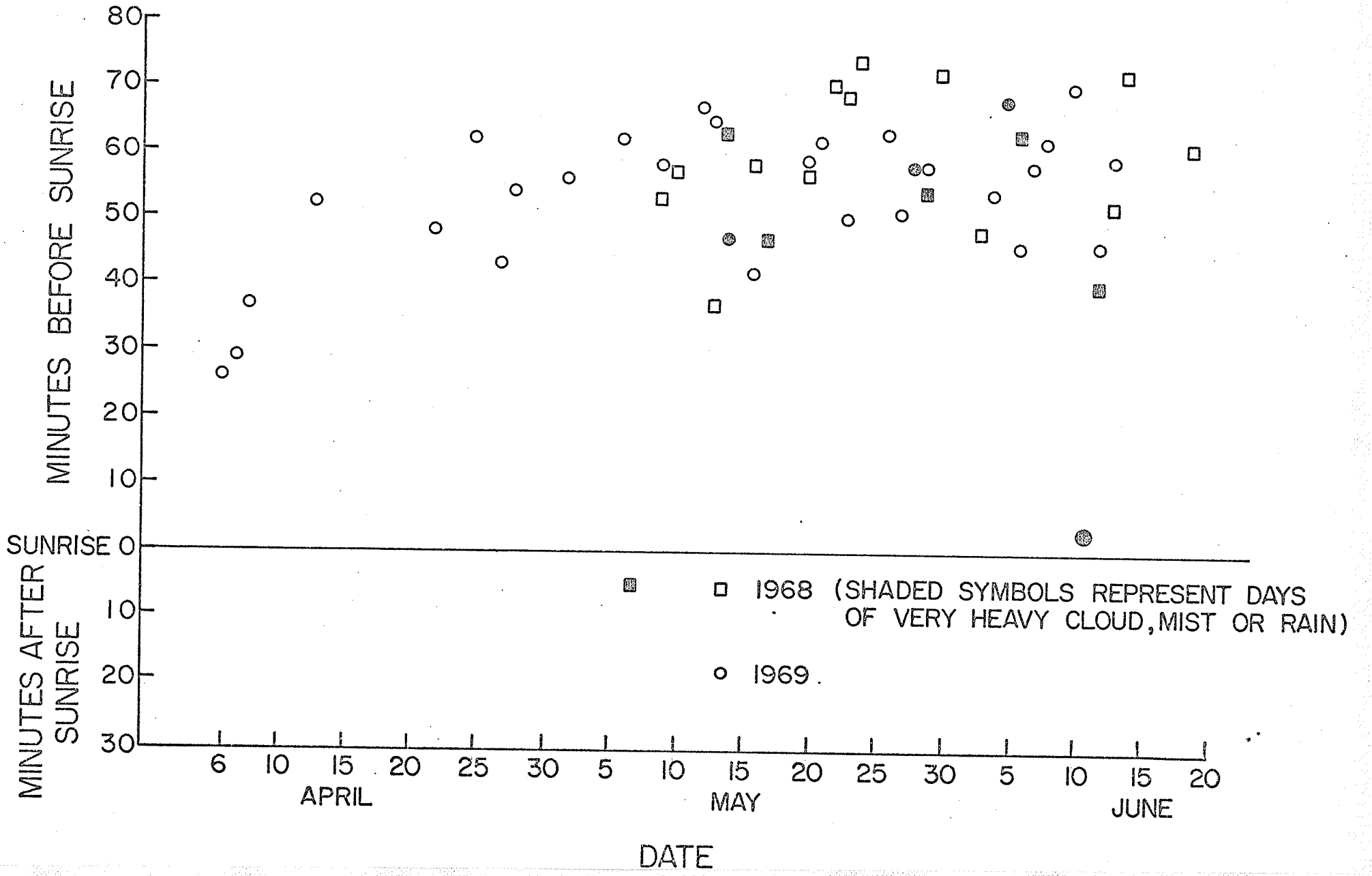
Times of Arrival on the Lek

The time of arrival of the first cock on the lek was recorded at the start of each morning observation period during May and June of 1968, and from April until June 1969. These values are expressed in Fig. 12 as moments before or after local sunrise. As Fig. 12 illustrates, the minutes

before sunrise that the cocks arrived on the lek increased during the first two weeks of April, and then remained relatively stable until the leks were abandoned in June, excepting for rainy mornings which in some cases delayed or precluded attendance. The progressively earlier arrival times relative to local sunrise recorded in the first weeks of April may correspond to the transition from arrival at sunrise to arrival at twilight, which Hjorth (1968) recorded for the Black Grouse, although at Hodgson it was more gradual than that observed by Hjorth, and not as closely related to the disappearance of the snow cover. In 1969 the snow cover on the open portions of the study area disappeared between April 9 and 13, and by that time the grouse had been arriving progressively earlier for at least a week.

Since it has been shown that gonadal activity, including spermatogenesis and hormone levels of the cocks decreased towards the end of the spring, (Nitchuk, 1969), it had been expected that the cocks might arrive later with respect to sunrise toward the end of the season than they had at the peak of activity. As Fig. 12 illustrates, this was not observed. A possible explanation for this phenomena has been advanced by Hjorth (1968) who found that while the arrival of the Black Grouse varied with the intensity of the incident light, they arrived at lower light intensities during the peak of the season than during the early or later

Fig. 12. Arrival times of male Sharp-tailed Grouse on leks at Hodgson during the spring seasons of 1968 and 1969.


MINUTES BEFORE SUNRISE
80
70
60
50
40
30
20
10
SUNRISE 0
MINUTES AFTER SUNRISE
10
20
30
□ 1968 (SHADED SYMBOLS REPRESENT DAYS OF VERY HEAVY CLOUD, MIST OR RAIN)
○ 1969
6 10 15 20 25 30 5 10 15 20 25 30 5 10 15 20
APRIL
MAY
JUNE
DATE

portions of the season. The fact that they arrived earlier relative to sunrise towards the end of the spring despite the tendency to require greater light intensities at that time was found by Hjorth (1968) to be related to the trajectory of the sun, which at that time lies at increasingly higher altitudes below the horizon. As a result, the light intensity necessary to bring the cocks to the lek is available at earlier times and the cocks maintain an early arrival time despite the increasing threshold necessary to activate them.

On smaller leks cocks were found to be less active than cocks on larger ones, and showed lower attachment to the lek (p. 72). Because of these findings, it was hypothesized that these differences would be reflected in the arrival times of the cocks. When statistically tested for 7 records on small leks and 20 records for large leks, it was found that no significant difference existed in arrival times (Fisher Exact Probability Test P = .45). This lack of behavioral difference is consistent with the lack of difference in testes volume, levels of cholesterol and spermatozoa, incidence of mitochondria and vascularization of the testes which were found by Nitchuk (1969).

During the spring of 1968, precipitation occurred on 21 days between April 10 and June 19. During the same period in 1969 precipitation was recorded on only 7 days.

Hjorth (1968) found that cloud cover affected the arrival time of the Black Grouse, and explained his results as being due to the lower light intensities on cloudy mornings. On the basis of Hjorth's findings, I tested the hypothesis that, due to the greater frequency of overcast skies in 1968, the arrival times for that year would have been later on the average than those of 1969. The arrival times were expressed as positive integers, and the 17 records for 1968 compared to the 22 records for 1969 by the use of the Median Sign Test. According to this test, no significant difference in arrival times existed (X^2 = .037; P > .05). The spring seasons of 1968 and 1969 were then analyzed in a similar manner, both individually and together, to determine if a significant difference in arrival times existed between rainy, cloudy, or misty mornings, and clear mornings. Again no significant difference in arrival times were found (Fisher Exact Probability Test P = .537, .183, for the spring of 1968 and 1969 respectively, and P >.05 by X^2 test for 1968 and 1969 combined). These results thus provide no evidence that Hjorth's (1968) findings are applicable to the Sharp-tailed Grouse.

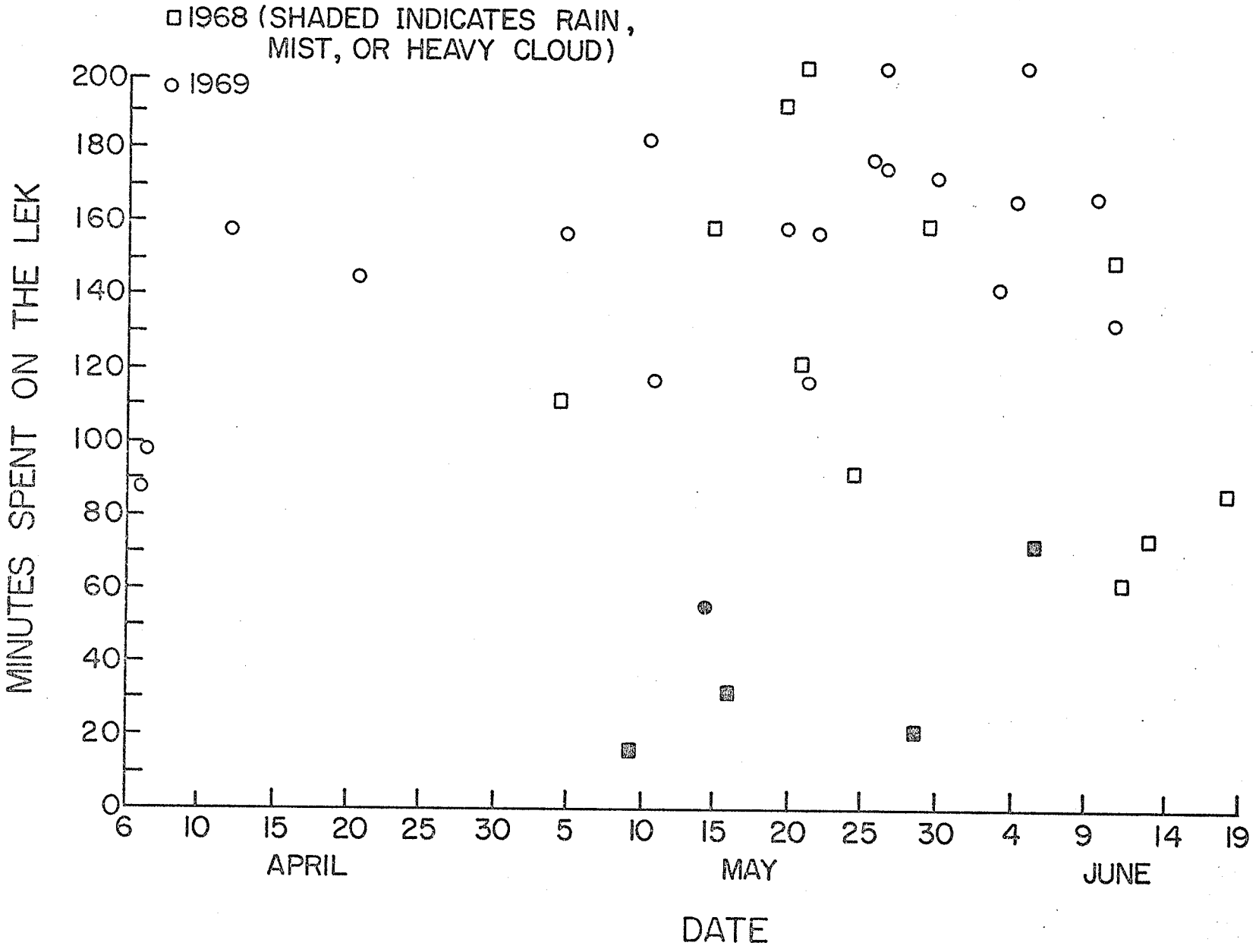
Time Spent on the Lek

The time spent on the lek was defined as the interval between the arrival of the first cocks as described above, and the departure of the last cock from the lek. As

above, small leks were compared to large leks for time spent on the lek, and again, for 13 records from small leks, and 36 records from large leks, no statistically significant difference was found (Fisher Exact Probability Test P = .454). Figure 13, which illustrates these data, indicates that the time spent on the lek increased during the early portion of the spring display period of 1969, and then remained at relatively constant levels except for major decreases on days with inclement weather. The longest days for both 1968 and 1969 were recorded in late May or early June. No decrease in time spent on the lek was noted towards the end of the breeding season, although display activity on the leks did decrease at that time. The considerable variation which occurred from day to day in time spent on the lek may have been due to several factors. One of these is the fact that several leks were included for each year in Fig. 13. These leks varied in number of cocks attending, location, surrounding vegetation on the lek, and other factors which might have influenced the time that the cocks spent on the lek. Visitations by predators which were undetected by the observer may have caused early departures from the lek on several occasions.

The Median Sign Test, and the Fisher Exact Probability Test were used to compare the time spent on the lek during 17 mornings in May and June of 1968 and 14 mornings

Fig. 13. Time spent on leks by male Sharp-tailed Grouse during the spring seasons of 1968 and 1969.


□ 1968 (SHADED INDICATES RAIN, MIST, OR HEAVY CLOUD)
○ 1969
MINUTES SPENT ON THE LEK
200
180
160
140
120
100
80
60
40
20
0
6
10
15
20
25
30
5
10
15
20
25
30
4
9
14
19
APRIL
MAY
JUNE
DATE

in May and June of 1969. Despite the fact that playbacks were used on several occasions in 1968 to bring cocks back to the lek, there was a significant difference ($P = .003$) between the two years, more time being spent on the lek during 1969. As was discussed above, the spring of 1968 experienced much more overcast weather than the spring of 1969. This difference in weather conditions may therefore account for the observed difference in time spent on the lek. These results, considered along with those shown in Fig. 13 and in the preceding section, suggest that for Sharp-tailed Grouse, time spent on the lek may be more subject to influence by rainy weather than are arrival times.

PRECOCIOUS LEK BEHAVIOR IN SHARP-TAILED GROUSE CHICKS

Introduction

Information gathered in this study, and by other workers (Schwartz, 1945; Hamerstrom and Hamerstrom, 1951; Lumsden, 1965), has established that juvenile Sharp-tailed Grouse are able to take part in the lek displays as early as their first autumn. The age at which these displays first develop, however, appears not to have been examined for this species. Although not an initial objective of this study, observations which relate to the early ontogeny of displays characteristic of lek behavior were made incidentally on very young Sharp-tailed Grouse and are described below.

Results

On June 14 and 15, 1969, while attempting to raise a group of newly-hatched Sharp-tailed Grouse, I observed on three separate occasions the precocious occurrence of the "dance" displays in 3 and 4 day old chicks. This phenomenon, which was reported for young Sharp-tailed Grouse by Ernest Thompson Seton (1940) has, to my knowledge, not been reported elsewhere. On the first occasion that I observed the "dance" display, the cardboard box in which the chicks were being held had been opened, and my hand had swept past one chick in order to pick up and remove another. As my hand

containing the captured chick was moving away, the first chick lowered its head, and with neck outstretched, beak slightly open, wings spread and curved downward, tail up, and feet stamping rapidly, followed my hand across the box. This behavior pattern appeared to be identical to the tail-rattling portion of the dancing ground display described by Lumsden (1965). This behavior was next observed on two occasions during the following day, when the chicks were four days old. On one of these occasions the behavior pattern was elicited in the same manner as described above; on the other occasion, simply by opening the box. Unfortunately the chicks died before more intensive observations could be made. It should be noted however, that despite this mortality, overt symptoms were not evident when the displays were observed, at which time the chicks were in apparent good health. Dissection showed the gonads to be less than 1 mm in diameter, and not hypertrophied.

Seton (op. cit.) described a brood of 15 chicks, therefore probably both male and female, which he raised under a domestic hen. All of these chicks first displayed without any obvious stimulus other than chilling, and subsequently were stimulated to display by Seton drumming his fingers against the pan on which they were being kept. He also described the chicks as crowing while performing the display. Seton's chicks were two weeks old when he observed

this behavior, and they persisted in the behavior for at least a week. My observations agree with Seton's completely, except that no crowing was perceived, and only one of the chicks danced at a time. The sex of the chicks involved was not determined with certainty.

Discussion

Fabricius (1962) described the pumping movements of young Shovellers (Spatula clypeata) and the chin lifting of young Eiders (Somateria mollissima) as being released by the same stimulus situation that evokes the following response, that is, an imprinting object of some kind. These same movements are known to be part of the sexual behavior of these species. It is possible that in the grouse observed by Seton and myself, the chicks were imprinting or imprinted to the hand, but since in the experience of both Seton and myself, the tail-rattling behavior was elicited on at least one occasion without the presence of the hand near the chicks, it seems unlikely that this behavior was necessarily directed toward an imprinting object.

The stimuli that elicited the bouts of tail-rattling seem to be more similar to the "stimulus contrast" or attention evoking stimuli described by Andrew (1964) who by presenting relatively intense stimuli to domestic chicks, produced various calls similar to those produced in chicks injected with testosterone. The fact that the pumping

movements of the Shoveller ducklings described by Fabricius (1962) occurred only when they were presented with a relatively large imprinting object such as a human, and not a relatively small imprinting object such as a balloon or a small box, would also support a stimulus contrast explanation for eliciting of these behavior patterns. Possibly a combination of the following response and stimulus contrast is involved.

In studying the development of adult responses in domestic chicks, Andrew (1964) also compared the reactions of normal and testosterone injected chicks toward an imprinting object. He concluded that in the courtship waltz and in copulation, two behavior patterns exhibited only by testosterone injected chicks, it is most probable that testosterone results in the development of systems of responses resembling those of the normal uninjected chick only by coincidence. In the same study, he concludes that applying terms descriptive of adult behavior to developing behavior is extremely difficult, and doubts that the central mechanisms governing sexual behavior are present in adult form at hatching. The fact that Sharp-tailed Grouse chicks can exhibit a complex behavior pattern similar to that shown by adult males on the dancing-ground indicates that in this species, one can relate such early behavior to adult behavior, and that the mechanism underlying at least some parts of

the complex behavior patterns associated with the courtship ritual are present at, or shortly after, hatching. The early occurrence of some motor components of adult displays suggests that a substantial part of adult sexual behavior may, in the chicks, lack only the motivational systems associated with increased testosterone levels to become integrated into true sexual behavior.

An alternative explanation for precocious tail-rattling appears to be that it is essentially an aggressive display, and therefore a typical response to a strange object. As in the Red Grouse of Scotland (Lagopus lagopus) (Watson and Jenkins, 1964), a considerable number of aggressive components are present in the courtship display of the Sharp-tailed Grouse (Lumsden, 1965). The tail-rattle display appears to be involved in the expression of this aggressive aspect of courtship, and is also used extensively as agonistic display between males on the dancing-ground. One occasion on which a female Sharp-tail with a brood gave a brief tail-rattle display, apparently as a distraction display, has also been observed (R. M. Evans, pers. comm.). Tail-rattling in such a context could hardly be described as courtship, but might well have aggressive components. Watson and Jenkins (op. cit.) describe one-day-old Red Grouse chicks attempting to "sing" on the ground in characteristic adult posture, and exhibiting several other adult-like aggressive

displays. They suggest that this may help to space the chicks, and mention that such displays occur often in caged chicks, but seldom in wild ones. Reactions towards an imprinting object which may have aggressive components including pecking, approach, and climbing on the imprinting object were reported for uninjected domestic chicks by Andrew (1964). Evans (1968) also found that aggressive responses can be elicited by a strange stimulus object, in both isolated and socially reared domestic chicks during the first few days after hatching.

These results suggest then that tail-rattling in Sharp-tail chicks, like aggressive reactions in domestic chicks, head bobbing or chin-lifting in ducklings, and "singing" in Red Grouse chicks, are all examples of aggressive behavior, differing from each other only in the degree of complexity of the behavior pattern exhibited. This hypothesis seems to agree with what has been observed, and perhaps offers a superior alternative to the first explanation that at least some of these responses are precocious sexual behavior. Possibly the ultimate explanation of phenomena such as precocious tail-rattling in Sharp-tailed Grouse involves elements of both the hypotheses presented here. In either case, however, it seems likely that the complex and highly competitive mating system of the Sharp-tailed Grouse may have favored the very early development

of many of the motor components of the displays associated with reproduction.

LEK ORGANIZATION, WITH SPECIAL REFERENCE TO TERRITORY

Introduction

The territories of lek grouse appear similar to those classified as "category C" by Nice (1941); that is, they resemble territories that function as mating stations only. The "sexual territory" defined by Tinbergen (1939) as "an area defended against other individuals of the same species shortly before and during formation of a sexual bond," also describes the lek territory. It should be noted, however, that although territories of lek grouse may be primarily "sexual territories" or "mating stations," such a classification is no doubt an oversimplification, since it is possible that they may also function in other ways, for example, in population control (Lumsden, 1965; Robel, 1970), or dispersion of the population (Wynne-Edwards, 1962; this study).

Hamerstrom and Hamerstrom (1955) compared large leks to small leks with reference to reproductive success. Schwartz (1945) in comparing large leks to small leks, suggested that the size of leks may be influenced by the number of cocks attending, the topography, and the height or type of cover. Similarly, Ammann (1957) found that the area included within a lek depended on its topography and the number of cocks attending it, but mentioned that individuals

on small leks (3 or 4 cocks) sometimes have very large territories. Several workers (Kruijt and Hogan, 1967; Lumsden, 1965; Schwartz, 1945; Evans, 1961), have also noted that territory sizes are generally larger near the periphery of the leks than they are near the center of the lek. The relationship between cover density and territory size has been studied for the Black Grouse (Koivisto, 1965), the Red Grouse (Watson, 1964), and briefly mentioned for the Greater Prairie Chicken (Schwartz, 1945), but does not seem to have been studied in the Sharp-tailed Grouse.

A part of the project at Hodgson was to extend these findings by comparing actual territory areas for leks of different sizes and cover types, and for individual territories within the same lek. In addition variations in territory size on the same lek over time, and stability of territories within and between seasons was examined. Finally, a model was postulated which attempts to integrate these observed behaviors into the functional context of the formation and maintenance of the lek display.

Small and Large Leks

For the purpose of analysis, leks were classified as "large" if they had 10 or more cocks regularly attending, and "small" if less than 10 cocks regularly attended. Nitchuk (1969) also used this classification system.

Several workers have described in some detail the

lek behavior of the Sharp-tailed Grouse on large leks (Ammann, 1957; Peterle, 1954; Evans, 1961; Lumsden, 1965), but few detailed studies of behavior on small leks exist. During this study therefore, relatively intensive observations were made on small leks with the aim of documenting the behavior of the attending cocks on these leks. The observations on large leks were generally in agreement with those of the workers mentioned above, and therefore will not be considered in detail here, except as they form a basis of comparison to small leks.

Behavior of Cocks on Small Leks: Of the four small leks studied, #5 and #10, which had only one and three cocks respectively, contained particularly large territories, averaging 424m^2, and the attending cocks appeared to exhibit a rather loose attachment to these territories. For example, cocks from these leks would on occasion display singly over a large portion of the fields in which their leks were located. On lek #10, where three cocks displayed, they possessed well established territorial boundaries on the portions of the perimeters of their territories that were adjacent to their neighbors. Despite this evidence of territoriality, however, two of these three cocks would often display singly at distances of 200-300m from the lek and, in the presence of a hen, these two cocks would abandon their territories entirely, and court the hen at some distance from the lek.

On several occasions one or both of these cocks courted the hen as she dust-bathed along the edge of the field in which the lek was located. The hen was observed on several occasions to enter the brush along the edge of the field, apparently to avoid their advances. These cocks were not observed to follow the hen into the brush, but remained in the open, displaying at the edge of the field. While following females, these two cocks on lek #10 would occasionally "face off" at one another in apparently typical boundary disputes, despite the fact that neither of them normally held territories within 100m of that area. In contrast to the behavior of these two cocks, the third male on this lek remained on its territory at all times. It is perhaps significant that despite the attentions of the two cocks that left their territories, the hens that were observed on this lek moved to the actual lek area where they remained for most of the time that they were observed. No copulations were witnessed on this lek.

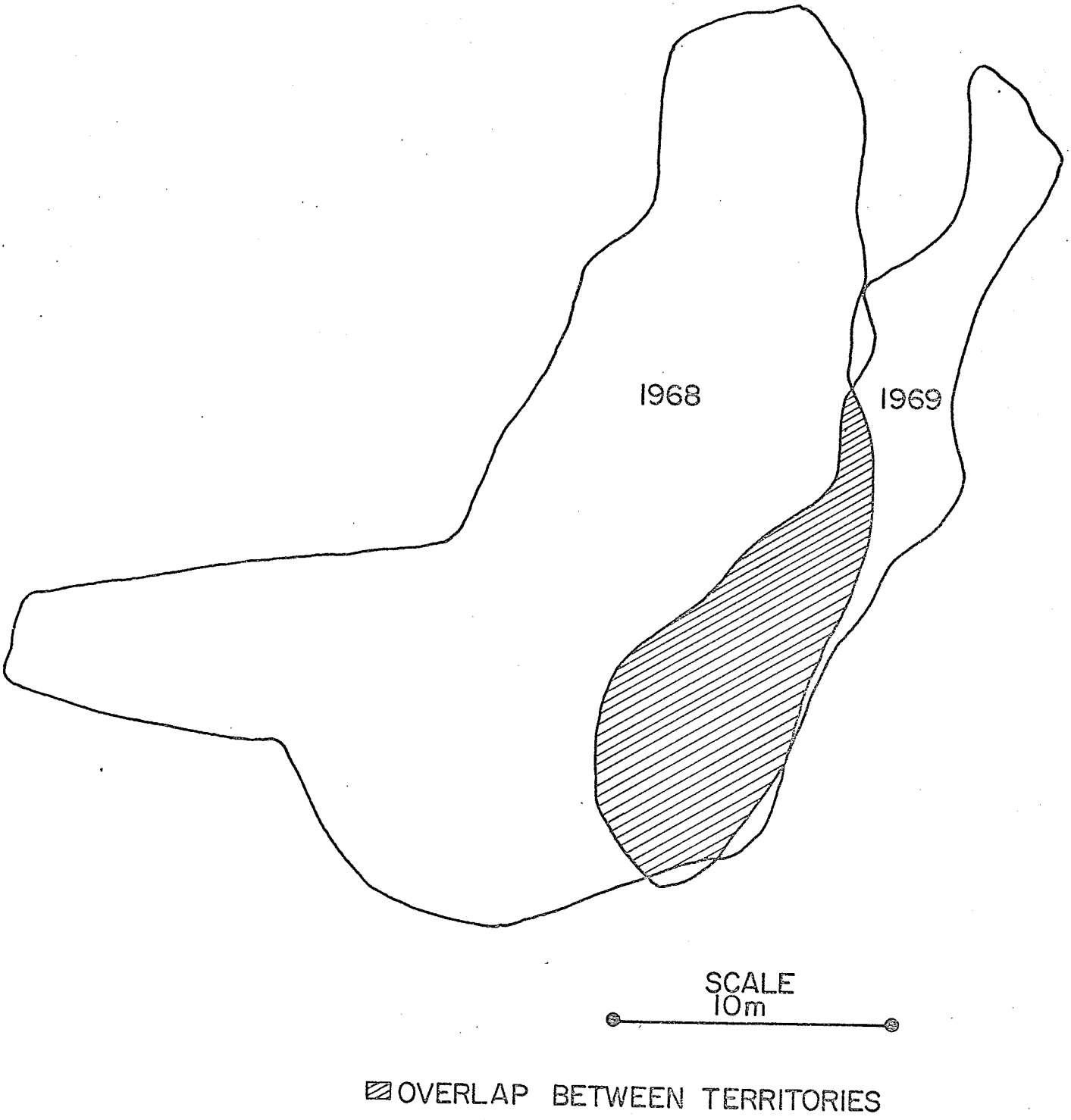
Despite the apparently low lek attachment exhibited by cocks on lek #10 during the morning display period, one of the three cocks from this lek whose territory was mapped in the spring of 1968, returned to the lek in the spring of 1969, indicating a strong stability between seasons. Since neither of the other banded cocks returned, and recruitment did not occur, this individual displayed alone. In spite of

the fact that the field in which this lek was located was 1/3 mi. long and $\frac{1}{4}$ mi. across, that fire had destroyed potential landmarks in the form of the stakes which had marked it in the previous spring, and that no autumn display had occurred on this lek, this single cock displayed on a territory which overlapped its former territory to a considerable degree (Fig. 14). It is of interest that this cock showed territorial stability without the presence of other cocks. Ammann (1957), reported that in his experience, only one instance of territorialism by a single cock had occurred, and this was based on a hunter's report. Surprisingly, the cock that displayed alone in 1969 was not the individual that had remained on his territory in 1968, but was one of the two cocks who frequently left their territories. This cock which was banded in the spring of 1968 as an adult was at least three years old in the spring of 1969.

The other two small leks, #33 and #35, which numbered 7 cocks each, showed no apparent territorial differences from larger leks, except for the difference in territory areas discussed below.

Territory Size Differences between Small and Large Leks: For 84 territories mapped at Hodgson, the average territory area was found to be $76m^2$, the smallest being $3m^2$ and largest $715m^2$. The mean area of 75 territories on 6 large leks was found to be $52m^2$, while 9 territories on 3

Fig. 14. Territories of cock number 115 on lek number 10 in the spring of 1968 and 1969.


1968
1969
SCALE
10m
OVERLAP BETWEEN TERRITORIES

small leks showed an average territory area of 239m^2. This difference was found to be statistically significant on the basis of Cochran's Modified "T" Test ($T = .287$; $P<.01$).

Behavior of Cocks on Large Leks: Extensive solitary displaying, such as that observed on the small leks #10 and #5, was not observed in cocks attached to large leks. Peripheral cocks occasionally pursued hens for considerable distances, and cocks occasionally pursued other males for short distances away from the lek, but typically the members of large leks remained on their territories during the display periods.

Large leks are typically organized in such a way that central and peripheral cocks exist. Nitchuk (1969), defined central cocks as those whose territories are completely surrounded by the territories of other cocks, and peripheral cocks as those whose territories are not completely surrounded. Small leks may also have central cocks, but due to the smaller number of cocks present they generally show a preponderance of peripheral cocks.

Dominance Hierarchy

It is known that in lek grouse, cocks whose territories are near the center of the lek are generally more successful in mating than peripheral cocks (Peterle, 1954; Ammann, 1957; Evans, 1961; Lumsden, 1965; Kruijt and Hogan, 1967). At Hodgson, all of the observed copulations were

performed by central males. As is suggested by the differences in mating success between cocks on the same lek, it is also well accepted that a dominance hierarchy exists between the cocks on a lek (Lack, 1939; Scott, 1942; Koivisto, 1965; Lumsden, 1965). Central cocks are thus near the top of this dominance hierarchy, while peripheral cocks are nearer the bottom. The existence of this radiating hierarchy from central to peripheral is further supported by the fact that at Hodgson, out of 86 cocks, the 63 adult males were found to be predominantly central in position (81%), while the 23 juvenile cocks were predominantly peripheral (78%) in their territory locations ($X^2 = 24.95$; $P < .005$). Juveniles did however occasionally occupy central territories (5 out of 23 juveniles observed on leks were central males), and in one case, a juvenile male located near the center of a large lek was observed to copulate with three hens in one morning despite the presence of adults around him.

No correlation was found between body weights and position on the lek, in 23 central and 18 peripheral cocks examined by difference of means "T" tests ($T = .0855$; $P > .05$). This evidence suggests that position on the lek, and thus probable position in the dominance hierarchy, is determined by some characteristic other than simple body weight.

Effects of Testosterone Injection

Nitchuk (1969), found that several physiological activities were greater in central cocks than in peripheral cocks. These included greater spermatogenesis and cholesterol levels in the testes, the latter indicating that greater testosterone levels exist in central than in peripheral cocks. The possibility of changing a cock's position relative to the center of the lek by changing its testosterone level was examined using a single bird, during the spring of 1969. The experiment consisted of injecting, on May 23, a juvenile peripheral cock (#159) which was practically non-territorial, with 5ml of 25mg/ml Testosterone hexahydrobenzoate. The injection was made into the thickest portion of the breast. This cock was observed the next day and was found to have greatly increased his general activity, spent much more time in territorial disputes with the cock immediately central to him, did not leave the lek frequently as he had done previously, and when a mounted hen was placed on his territory he was observed to copulate with it 45 times in 50 minutes. During this time the mounted hen first had its head broken off, and then was turned upside down, without the injected cock lessening its copulatory activity. Peripheral cocks were not observed to copulate with models on other occasions, and even central cocks were not observed to copulate so vigorously with a mounted hen. On the first

occasion that the injected cock mounted the model, copulation was interfered with by an adjacent cock whose territory was more centrally located, but thereafter, there was no interference. Even when the other cocks were alert due to the observer's movements in the blind, the injected male continued tail-rattling around and near the mounted hen. This increased activity was observed again on June 4, although not to such a marked degree. On June 4, this cock remained near the lek, tail-rattling for 15 minutes after the other cocks had left. Despite this increase in its activity which was noted in this individual after testosterone injection, no change in the inner boundary of his territory was observed.

One explanation for the above results is that testosterone levels are not related to the position of a cock on the lek. Nitchuk's results discussed above, however, strongly suggest that testosterone levels are at least correlated with position on the lek. A more likely explanation might be that testosterone levels alone are not responsible for dominance and hence position on the lek. A third explanation might be that by late May, when this experiment was conducted, territories are so well established, and local dominance within these territories so strong, that hormone changes which might actually alter the dominance hierarchy were not sufficient to effect changes in the

territorial arrangement of the lek. This third hypothesis has the merit that it could readily be tested by altering hormone levels earlier in the spring season, before territories are firmly established.

Territory Size Differences Between Central and Peripheral Cocks

In order to obtain quantitive data on the size of territories in peripheral cocks (those cocks not completely surrounded by others) compared to central cocks (those cocks whose territories are completely surrounded), the areas of 60 central territories and 17 peripheral territories were compared. The average size of peripheral territories was found to be $108m^2$, while the average size of central territories was only $43m^2$. This difference was found to be significant by the Cochran's Modified "T" Test ($T = 2.054$, $P < .05$).

Leks with Tall Vegetation Compared to Leks with Short Vegetation

Watson (1964), working with the Red Grouse of Scotland, found that the territories of the cocks tended to be larger in open areas with little cover than they were in areas where the cover was taller and heavier. Watson suggested that this occurred because the cocks could see each other at greater distances where the cover was open. Koivisto (1965) found a similar relationship between cover

and territory size for the Black Grouse.

During this study, the territory sizes of 51 central males were compared on 9 leks, 5 of which were on mowed grass or ploughed sites, and 4 of which were on alfalfa or grass-brush sites. By means of Cochran's Modified "T" test, it was found that a significant difference ($T = 2.605$, $P < .01$) in mean territory size existed between these two groups, the territories of cocks on open leks being smaller than those on leks with tall and heavy cover. This result, which is the opposite to that found by Watson (1964) or Koivisto (1965) is discussed further below (p. 97).

Besides the territorial differences noted above it was also observed that cocks on leks with alfalfa cover were apparently less active than those on leks with more sparse cover. Alfalfa in some cases hindered the movements of the cocks which appeared to contribute to reduce activity on these leks. Because of its rapid growth in spring, it seems likely that alfalfa may on some leks actually reduce reproductive efficiency with regards to renesting hens should they return to the lek in late May or early June.

Territorial Stability

If the territory of the same cock is measured on two different occasions, various degrees of stability may be observed; for instance his territory may have moved from one location to another, or the outer boundary of all or part of

the territory may have shifted to some extent, altering the territory. In an attempt to examine territorial stability over time, an index of stability was devised to give a single meaningful expression for the stability of a territory as measured by changes in the location, size or shape of the territory.

Index of Stability: To obtain a measurement of the change in location of a territory, some expression was necessary which would describe the distance that the territory moved. To measure this distance moved, a point most representative of the territory's location was needed. The "center of gravity" of the territory was used as this point.

Area changes in a territory were measured from maps using a polar compensating planimeter. Changes in shape of a territory are typically reflected by changes in the relationship between the area and perimeter of the territory. As an index of these changes, an expression which has been developed in limnology (Hutchinson, 1957) for studying shoreline development was used: $\frac{L}{2\sqrt{\pi A}}$ where "L" is the perimeter of the territory in meters, and "A" is the area of the

territory in square meters.

Incorporating the three parameters the following index of stability was derived:

$$\text{Index of Stability} = \frac{D^2 + |A - A'|}{A + A'} + \left| \frac{L}{2\sqrt{\pi A}} - \frac{L'}{2\sqrt{\pi A'}} \right|$$

where "D" is the distance that the territory moved as measured by the distance between the centers of gravity, "A" is the area of the territory on the first occasion, "A'" is its area on the second occasion, "L" and "L'" represent the perimeter of the territory on the first and second occasions respectively. The distance moved was squared to permit cancellation of units. This procedure also provided a weighting for location, which, of the three variables examined, appears to be the most directly related to territorial stability. The first term of the equation was divided by A + A' to make distance moved and area changes relative to the size of the area involved. It was also useful in that it resulted in a complete cancellation of units. Since the amount of change regardless of sign was the value wanted, absolute values were used for changes in area and shape. Any changes in these parameters, or in the distance moved, would therefore always result in a positive value for the stability index. The magnitude of the calculated index of stability varied inversely with the stability of the territory in question, that is, the more unstable a territory, the larger the index

of stability.

In using this index to measure the stability of a territory, the territory was first mapped on a given occasion, the parameters A, and L recorded, and the center of gravity found in the manner described above. At a later date, the territory of the same color-marked cock was mapped again and the new area (A'), perimeter (L') and center of gravity were recorded. The distance moved (D) was then found by measuring on a map, the distance between the two centers of gravity. Having obtained values for A, A', L, L', and D, the index of stability could be calculated by using the equation described above. To facilitate calculations, a program was made which allowed easy calculation of the index of stability on a desk computer.[1] Using this method, an index of stability was calculated for all those cocks whose territories were measured on more than one occasion. The indices of stability obtained for a number of territories were then analyzed statistically. The testswere conducted by ranking the indices according to magnitude, and then employing the Median Sign Test. Levels of significance were calculated by either the X^2 test or the Fisher-Exact Probability Test.

Results: Indices of territorial stability were used to compare stability between early and late spring, and to

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[1] Olivetti Programma 101 Desk Computer.

compare stability between seasons with stability between two occasions during one season. Average, median and range of indices and the average number of days between the two territory mappings used to compute the indices, are listed in Table VI. In the case of stability between early spring and late spring, for 5 territories measured at least twice before the peak of lek activity on April 28 and 8 measured at least twice after the peak, it was found that the stability between the two occasions before the peak of mating was lower than the stability between the two occasions after the peak of mating ($P = .035$, Fisher Exact Probability Test).

Pre-peak and post-peak spring stability data were also combined and compared to stability indices obtained between seasons; that is between spring and fall or between two consecutive spring seasons. Stability between seasons was estimated by comparing the last measurement of a particular cock's territory in one season to the first measurement of the same cock's territory in the next season. Where one cock's territory was measured on more than two occasions during a spring season, the largest stability index value for that individual was used. In this way, the spring data was biased towards instability if at all. When these indices were compared, it was found that for 13 territories measured within spring and 17 territories measured between seasons, stability within the spring season tended to be

TABLE VI

Comparison of between and within season indices of territorial stability for Sharp-tailed Grouse at Hodgson in 1968 and 1969

Period Measured	#Birds	Number of Territories	Average #Days Between Measurements	Stability Index Average	Stability Index Median	Range
Early spring	3	5	10	1.355	1.417	.674 - 1.992
Late spring	8	8	21	.702	.846	.286 - 1.142
Within spring season	15	13	17.7	.905	.878	0 - 1.991
Between seasons*	11	17	--	185.266**	3.041	.195 -1385.340

*Between spring and fall, fall and spring, and spring and spring.

**The average stability index is much larger than the median in this group because of 5 cocks which moved from one lek to another over considerable distances, thus producing very high indices of stability.

greater than stability between seasons (P = .009, Fisher Exact Probability Test).

Use of Landmarks

At the time of the earliest mapping of territories on lek #2a, (April 6, 1969), territories were already well established despite the presence of at least a foot of drifted snow over the lek. These territories were mapped on both April 6 and 7 and found to be stable between these dates.

Anderson (1969), who observed Prairie Chicken on a lek which had been suddenly covered with snow on April 23, also observed little or no changes in size or location of territories. It seems possible, however, that in the case of the Prairie Chickens, they may still have had the lek markers, which Anderson used for mapping territories, as landmarks. On April 8, the grid which was used to map the territories on lek #2a at Hodgson (see Methods, p. 26) was moved 10m north, as was the blind from which the grouse were observed. The blind and the wooden stakes which made up the grid were the only stable landmarks within 200m of the lek, and it was hypothesized that the cocks were using them as landmarks in setting up their territories. If this hypothesis was true, the territories would presumably shift 10m north along with stakes and blind. When the territories were mapped on April 8, the day after the stakes had been

shifted, it was found that they were on the same locations as they were on April 6 and 7, unaffected by the stakes or the blind which had been moved. With the rapidly melting snow, and my own tramping with snowshoes, the topography of the lek changed each day, therefore it is unlikely that the grouse were using immediate landmarks such as lek topography for stabilizing their territories. This experiment suggests that Sharp-tailed Grouse are able to maintain stable territories without the aid of any permanent landmarks closer than 200m.

Direction of Interactions

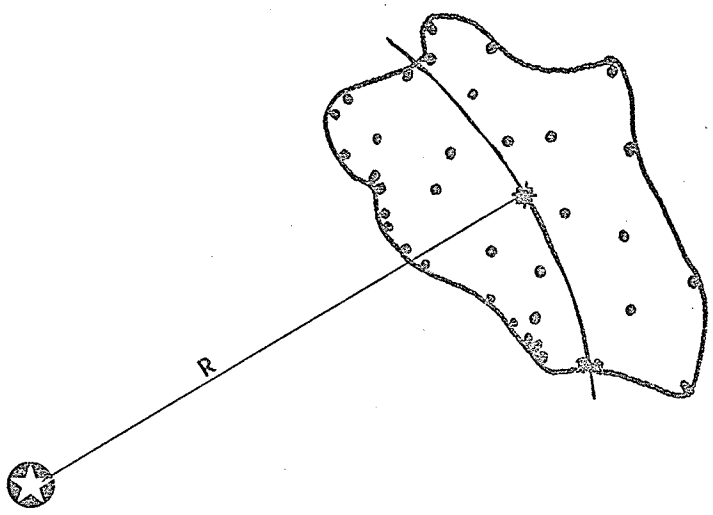
Several investigators (Rippin, 1970; Anderson, 1969; Evans, 1961, 1969; Robel, 1965, 1967; Kruijt and Hogan, 1967) recorded the locations of cocks on the lek over a period of time, to assess territory locations and boundaries. The further possibility that the compactness and apparent cohesion between birds which seems to be typical of most leks might be assessed by examining the directionality of these interactions, however appears not to have been considered previously. Directionality of interactions was assessed in this study by determining the proportion of interactions directed towards the center, compared to those directed towards the periphery of the leks at Hodgson, as described below.

In mapping the territory of any cock, the procedure

followed was to plot numerous locations of the cock on the lek, and then with particular reference to boundary disputes, to delineate his territory (see Methods, p. 26). Using these locations it could be determined which parts of the territory were most frequently occupied. To assess whether various cocks tended to display primarily towards, or away from the center of the lek, the number of locations on the half of the territory closer to the center of the lek was compared to the number of locations on the outer half of the territory. The center of the lek was measured as either the geometric center of the lek or the center of gravity of the territory of the dominant cock when this individual was known. These two methods generally agreed closely; where minor discrepancies were present, the center of gravity of the dominant was taken as the most relevant point. When the center of the lek had been determined, a compass point was placed at the center of the lek, and an arc drawn through the mapped territory of each cock. In all instances, the radius of the arc was equal to the distance from the center of the lek to the center of gravity of the territory being measured (Fig. 15). The number of plotted locations inside the arc were then compared to the number of locations outside the arc. Locations falling on the arc were counted as being outside the arc.

If the locations of the cock were distributed

Fig. 15. Sample territory of a male Sharp-tailed Grouse illustrating the method used to determine the proportion of locations away from the center of the lek and towards the center of the lek.



SCALE

10 m

CENTER OF LEK

CENTER OF GRAVITY OF TERRITORY

R DISTANCE FROM CENTER OF LEK TO CENTER OF GRAVITY OF TERRITORY

PLOTTED LOCATIONS OF COCK

randomly throughout its territory, the above method would have yielded a preponderance of locations on the outside of the arc, since points falling on the arc were considered as being outside, and generally, the greater portion of the territory fell outside the arc. Despite this bias, it was found that for 49 central cocks, excluding those whose territories encompassed the center of the lek, and also for 26 peripheral cocks, a significantly greater proportion of locations were towards the center of the lek (Diff. of Means "T" statistic, $P < .005$ for both peripheral cocks and central cocks). In addition, it was found that the peripheral cocks showed a greater proportion of locations towards the center of the lek than did the central cocks (Table VII, Median Sign Test $X^2 = 6.5856$, $P < .05$).

TABLE VII

Comparison of central and peripheral cocks with regard to the number of locations towards the center of the lek

Position of Cock	Number of Territories	Locations towards the center			
		Average#	Percent	Median	Range
Central	49	20	54.3	20	6 - 32
Peripheral	26	25	67.5	25	3 - 36

Four Hypotheses of Lek Formation and Maintenance

As has been stated above, the average territory size on small leks is greater than the average territory size on large leks, peripheral cocks generally possess larger territories than central cocks, and territories on leks with heavy cover are generally larger than those on leks with little or no cover. In addition, cocks tend to concentrate their activities towards the center of the lek. In an attempt to interpret these results, a set of four hypotheses for lek formation and maintenance were postulated which can be described as follows:

The Hypotheses:

1. Sexually active Sharp-tailed Grouse cocks are attracted to one another individually or as groups. In a displaying group, a cock will be attracted towards the source of greatest stimulation visually or auditorally, and thus will be attracted towards the center of the group, which in lek species will also be the center of the lek.

2. As well as being attracted to one another, the cocks have an individual distance within which they will attempt to repel other cocks.

3. The cocks exhibit a dominance hierarchy within the group; that is, some males will be more able to reach the area which they are attracted to before being repelled by a more dominant male. This dominance hierarchy would

initially result in the more dominant males getting closer to the center of stimulation than the others.

4. The formation of territories, with the accompanying home ground advantages and local dominance accrued by the territorial bird, would temper the dominance hierarchy and make further changes in territorial configuration difficult, thus stabilizing the lek.

Evaluation: Several of the above hypotheses appear to be well documented; for example the tendency (No. 1 above) for lek grouse to display as a group. Once such a group is formed it follows that the greatest concentration of auditory and visual stimulation provided by members of the group will be at its center. The hypothesis that Sharp-tailed Grouse are attracted to the source of greatest stimulation has not been verified experimentally; but, besides being a logical deduction, since something attracts the birds to the group, the hypothesis is consistent with the view (Grange, 1948; Hamerstrom and Hamerstrom, 1960; Lumsden, 1965; Robel, 1967) that one function of the lek is to provide greater stimulation to attract females for mating.

As discussed by Emlen (1952), most individuals in bird groups exhibit centrifugal as well as centripetal tendencies; those tending to keep individuals apart being manifested as some form of individual distance (No. 2 above).

The existence of agonistic behavior when one cock encroaches on the territory of another, seems to constitute evidence for this type of behavior on the lek.

With reference to the third hypothesis, several investigators have concluded that a radiating hierarchy exists in lek species (Lack, 1939; Scott, 1942; Koivisto, 1965; Lumsden, 1965). The fact that central males do most of the mating, and are predominantly adult, with juvenile cocks generally being peripheral also supports the suggestion that more dominant cocks tend to be at the center of the lek, as does the greater degree of testis development in the central males (Nitchuk, 1969).

Hamerstrom (1939), Koivisto (1965), and Robel (1967), found that early in the spring, stability of territories was lower, and fighting more frequent, than later in the season. Their findings therefore tend to support the fourth hypothesis above. This hypothesis is also consistent with the fact that territories at Hodgson became more stable as the spring season progressed, and also with the finding that late in the season, testosterone injections, which might be expected to influence dominance changes, did not effect changes in the territorial configuration of the lek.

The above results suggest that the present set of hypotheses are entirely consistent with existing

evidence. Although they will no doubt require modification as more data become available as discussed above, they appear to provide a useful conceptual framework within which to consider lek behavior.

Discussion

Because all the cocks, according to these hypotheses, are assumed to be attracted towards the center of the lek, it follows that birds immediately central to the peripheral cocks will respond defensively against the centrally directed activities of the peripherals. While this would be expected to limit the territory size of the central birds, it would not limit the outer boundary of the territory of peripheral birds even if central birds did force peripheral males outwards. Within the context of these hypotheses, therefore, it is evident that peripheral cocks have little "pressure" on their territories except perhaps from adjacent peripherals. "Pressure" in this sense refers to the tendency of neighboring cocks to encroach on the individual's territory, and therefore the vigor with which he must maintain his territorial boundaries. The inward "pressure" created by the attraction of the cocks towards the center of the group, but opposed by the individual distances or territoriality of the cocks, would create a situation analogous to the rubber disc model described by Huxley (1934), or to a shallow inverted cone into which water-filled balloons are released.

In both of these physical models, a compression of the more central discs or balloons would occur due to the greater pressure exerted on them.

Central cocks, unlike peripherals, are entirely surrounded by other cocks. Like peripherals they are attracted towards the center of stimulation, and hence also act offensively towards any cocks located even closer to the center of the lek. As well as acting offensively towards the center of the lek, they must act defensively towards encroaching peripherals and lateral neighbors. Being surrounded by others, these cocks may be thought of as having more "pressure" on their territories than do the peripherals, who are not so surrounded. Since these individuals would have to act agonistically over a greater proportion of their territorial boundaries in order to maintain their territories, it would seem probable that their territories would be contracted relative to the peripheral cocks, and this in fact was observed (p. 80).

According to the above hypotheses, cocks located at or very near the center of the lek would have no polarity of action, since the stimulus concentration is the same all around them. These individuals thus act predominantly defensively against encroaching cocks, the presence of which should result in the relatively small territory size actually characteristic of central cocks.

The fact that larger leks have smaller territories on the average than do smaller leks can be explained within the context of the above hypotheses by the lower attraction towards the center of the smaller leks, resulting from the lower stimulus intensity produced by the smaller number of cocks present. The greater proportion of peripheral compared to central cocks on small leks would also be expected, from these hypotheses, to lead to larger average territory sizes, since a greater proportion of the cocks on small leks would have undefended outer boundaries. Further, the central cocks on small leks, being surrounded by fewer rivals, would perhaps be able to defend larger territories.

The data showing differences in territory size on leks with heavy cover compared to leks with low cover can also be explained on the basis of these hypotheses. In a situation such as a lek, where the group formation is most likely dependent on the attraction of the individuals to one another, any reduction in the ease with which the cocks saw or heard one another would lead to a lowering of their attraction towards one another or the group. In this situation, less "pressure" towards the center of the group would exist, and the territories of central cocks could expand accordingly. The lek with heavy cover creates such a lowering of visual and auditory stimuli, and thus might be expected to contain larger territories than a lek where cover did

not interfere with interactions.

Another factor which might allow larger territories to be held on leks with dense cover might be the presence of heavy vegetation at the boundary between two adjacent cocks. This boundary would not need to be defended, and hence each cock would presumably have more time to defend the remainder of its territorial boundary, with the possible result that it would therefore be able to defend a larger territory.

The fact that hens move to the center of the lek for copulation can also be explained by these hypotheses merely by assuming that hens, like cocks, are attracted towards the area of the greatest stimulation, and thus towards the center of the lek. On the other hand, the hens could simply be attracted to the most dominant males, whose territories will be near the center of the lek.

Since hens do tend to allow copulation near the center of the lek, and since on the lek, the only unique position which can be competed for is the center, the above hypotheses would form a workable unit in which a competitive mating system could operate and be perpetuated by the successful reproduction of the centrally located females and dominant males.

INTERSPECIFIC INTERACTIONS

Raptors

Several investigators have suggested that the exposed nature of the lek, the considerable amount of time that the males spend on the lek, and the preoccupation of the cocks while displaying, make them particularly vulnerable to predators, especially raptors, while on the lek. Lehmann (1941), advanced the opinion that Attwater's Prairie Chicken (*Tympanuchus cupido attwateri*) were probably heavily preyed upon during their display periods as a result of their preoccupation while on the lek. Hart *et al.* (1950) observed a coyote hidden in the weeds on a lek rush out and capture a cock. Hjorth (1968), studying the Black Grouse suggested that female Goshawks (*Accipeter gentilis*) could be a serious threat to cocks on the lek. Ammann (1957) on the other hand, pointed out that while kills on leks by avian predators were not uncommon, such losses were not inordinately high, considering the amount of time that the cocks spend on the lek.

Berger, Hamerstrom and Hamerstrom (1963) did a comprehensive study of the effects of raptors on Greater Prairie Chicken leks. Out of 4,745 morning observations, 1,379 encounters between prairie chicken and raptors were recorded. Out of all these interactions only three resulted in the death of a prairie chicken. Circumstantial evidence

suggested that at least three, and possibly six more raptor kills occurred on leks. In addition, there were two pursuits which ended out of sight of the observers. The species responsible for the known kills were the Harrier (Circus cyaneus), the Great-Horned Owl (Bubo virginianus), and the Snowy Owl (Nyctea scandiaca).

During this study, 17 raptors were observed near active leks during 100 periods of observation, including both morning and evening periods (Table VIII). Circumstantial evidence, described below, was obtained which indicated three kills or attempted kills by raptors on leks during this time. In no case was a predator actually observed making a kill. Interactions between raptors and Sharp-tailed Grouse on the lek were witnessed on 17% of the occasions spent observing the leks. The actual percentage may be greater than this figure, since the observer's field of vision was restricted by the blind. In 15 of 17 interactions that were noted, the species of raptor was identified. Of these 15 interactions, 10 (67%) involved Harriers. Berger et al. (1963) found Harriers to be involved in 64% of their raptor-Prairie Chicken encounters. Goshawks were involved in two (13%) of the observed interactions at Hodgson. A Great-Horned Owl was seen on one occasion and one Red-tailed Hawk (Buteo jamaicensis) and one Kestrel (Falco sparverius) were observed.

Reactions of Raptors: The 17 observed interactions

TABLE VIII

Reactions of raptors and grouse during raptor visits to lek

Raptor species	Reactions of raptors				Reactions of grouse[1]			
	Attack	Interest[2]	No Interest	#Inter-actions	Flush	Squat	No Reaction	#Inter-actions
Harrier (*Circus cyaneus*)	2[3]	2	5	10	4[3]	4	1	9
Goshawk (*Accipeter gentilis*)	1	1	--	2	1	--	--	1
Great-Horned Owl (*Bubo virginianus*)	1	--	--	1	1	--	--	1
Red-tailed Hawk (*Buteo jamaicensis*)	--	--	1	1	--	1	--	1
American Kestrel (*Falco sparverius*)	--	--	1	1	1	--	--	1
Unidentified hawks	--	1	2	2	--	--	2	2
Total	4	4	9	17	7	5	3	15[4]

[1] "Reactions of grouse" represents the behavior of the majority of birds on the lek.

[2] "Interest" describes occasions when the hawk approached the lek or otherwise showed apparent interest.

[3] The same Harrier repeatedly harassed the same flock of grouse on a lek for two consecutive days.

[4] Two raptor visits to leks occurred when no grouse were on the lek (see text).

between raptors and cocks on the lek included four attacks, four occasions when the raptor showed apparent interest in the cocks, and watched the grouse from the ground, and seven occasions in which the avian predators showed no apparent interest, merely flying past the lek. On two occasions, the raptors' reaction was not noted (Table VIII). The species of raptors and their frequency of observation are also shown in Table VIII.

The four attacks involved two by a Harrier, one by a Goshawk and one by a Great-Horned Owl. The attack by the Great-Horned Owl occurred on May 16 at 5:11 A.M., 29 minutes after sunrise on a heavily overcast day. The owl first landed near a grouse mounted in the squatting position (see Methods, p. 12) which was located approximately 100m from where three cocks were actively displaying. After standing near the mounted grouse for approximately one minute, the owl flew directly towards the displaying grouse, who flushed at the last instant and escaped. Berger et al. (1963), on the basis of their extensive study of the Greater Prairie Chicken, concluded that Horned Owls represented one of the most serious raptorial predators of grouse on leks (see also Ammann, 1957; Hjorth, 1968). Berger et al. (1963), attributes the success of Horned Owls in part to their capabilities, and in part to the time at which they hunt, which overlaps with the early arrival of cocks on a lek, when the cocks

presumably are more vulnerable than later in the day when the light is better. This suggests that if the owl's attack which I observed had occurred 15 minutes earlier, when light was less intense, and when the grouse were actively displaying, it might well have been successful.

The attack by the Goshawk was unusual in that it appeared to have been elicited by sound alone. The attack occurred at 5:25 A.M. on June 4, 1968, approximately one hour after sunrise. A tape recording of displaying grouse was being played back at the time in order to attract cocks to the lek (see Methods, p.25). No live or mounted grouse were on the lek at the time. The hawk flew directly toward the lek at an altitude of about 4 ft., with rapid wing strokes. This hawk was accidentally caught in a mist net which was erected on the lek, hence it was not possible to determine whether or not it would have approached the loudspeaker.

The attacks by Harriers involved a male Harrier on two subsequent days at the same lek. The attack patterns exhibited by the Harrier on these two days was nearly always the same, and consisted of a low approach, then a rise and a swoop down at the grouse. This approach was used even when the grouse were perched in trees. The grouse consistently remained still until the instant that the hawk started its swoop, then they flushed. Although direct evidence is

lacking, the similarities in the behavior of the Harrier on both days suggests that it was probably the same hawk in both cases. On both days the hawk repeatedly attacked the grouse both on and off the lek and, I believe, effectively prevented them from displaying for any length of time.

Others have also recorded such harassment by Harriers: Schwartz (1945), for example found that Harriers frequently disrupted Greater Prairie Chicken leks, while Lehmann (1941) suggested that harassment by Harriers was the greatest disruptive influence on the lek activities of the Attwater's Prairie Chicken. Berger et al. (1963) observed some instances in which Harriers harassed leks persistently enough to interfere with breeding behavior, but such instances were uncommon.

Of the nine instances in which the hawks apparently ignored the grouse on the lek, five involved Harriers, one involved a Red-tailed Hawk, and one involved an American Kestrel (Table VIII).

Of the four instances observed in which the raptor showed non-aggressive interest in the displaying grouse, one involved a Goshawk, two involved Harriers, and one involved an unidentified hawk. Both the Harrier and the unidentified hawk landed approximately 100m from the displaying grouse, in plain view of them and remained, apparently watching, for 15 - 20 minutes before flying away. Both times the grouse

apparently ignored them. Another Harrier showed aggressive interest in a mounted grouse, swooping from about 15 ft. to about 3 ft. above a grouse model mounted in the squatting position. The hawk then continued on its way. There were no live grouse on the lek at this time, and no playback was being used. The Goshawk, which also displayed apparently non-aggressive interest, flew directly onto the lek, flushing the grouse. It then stood on the lek for nearly an hour, and did not attack, even when the cocks returned and resumed their display, some within 5m of the hawk. Such behavior by grouse towards Harriers has been seen (Berger et al., 1963), but to my knowledge it has not been observed towards such a powerful raptor as a Goshawk. Berger et al. (1963), found it noteworthy that on one occasion during their study, a Goshawk exhibited such non-aggressive interest, but the cocks did not return to the lek until after the Goshawk had left.

Reactions of the Grouse: The reaction of the grouse to an approaching avian predator seemed to vary with the species of raptor and the nature of its approach. In nine instances involving Harriers, the grouse flushed four times, squatted four times, and showed no reaction on one occasion (Table VIII). The Goshawk and the Horned Owl, each involved in one interaction, both elicited complete flushes of all the grouse on the lek. As mentioned above, the cocks later

returned to the lek and displayed to within 5m of the Goshawk. The Red-tailed Hawk, involved in one interaction, elicited a squat response in the grouse, but none flushed.

My assistant, Mark Mattson, reported a complete flush of the cocks on a lek when a Kestrel approached. The Kestrel perched for several minutes on a post set up on the lek. The grouse returned after the Kestrel left. It seems likely that the falcon silhouette and wing beats of the Kestrel, set against the open sky where it is difficult to judge size, caused the grouse to mistake it for a larger falcon species such as the Peregrine (Falco peregrinus), which is known to produce strong fear responses in Prairie Chicken (Berger et al., 1963). This interpretation is in agreement with that of Berger et al. (1963) who observed the same phenomenon.

Raptor Predation on Leks: None of the observed interactions resulted in a raptor kill, but circumstantial evidence was obtained that indicated four attempted or successful raptor kills on Sharp-tailed Grouse leks.

On May 6, 1969, a female Harrier was seen to land near the edge of an active lek, and pick at the remains of a banded cock Sharp-tail, which appeared to have been killed several days previously. The kill was approximately 15m from the known territory of that cock. As there were no feathers on the lek, it was hypothesized that a raptor

approached, that the grouse flushed, and that one cock was captured shortly after flushing or attempting to flush. The cock which was killed had been injured in a cannon netting a week previously, and had been unable to fly properly when released. This injury may have contributed to his death. Berger et al. (1963) suggested that raptors may visit leks for the precise reason of possibly capturing an injured or sick bird.

Circumstantial evidence for another kill or attempted kill by a raptor was found on a lek located 600m from the lek upon which the injured cock was killed. On this lek, a large patch of grouse feathers was found, along with one raptor feather, which has tentatively been identified by microscopic comparison with museum feather specimens as belonging to a Goshawk. No remains were found on or near the lek, so either the Goshawk carried the grouse off, or the grouse escaped after a struggle in which the hawk lost a primary feather.

In another area a large patch of grouse feathers was found on a spot of open, heavily grazed pasture about 100m from an actively used lek. The size of the feather patch suggested a successful kill. Since there were no power lines, trees, or other hazards nearby, and since Sharp-tailed Grouse prefer heavier ground cover for a roosting place (Ammann, 1957), it seemed probable that the feathers were due to a

Sharp-tailed Grouse being struck there by a raptor after being flushed from the nearby lek. Since no remains were found with the feathers, another, and possibly more likely explanation might be that the grouse might have been struck by a Horned Owl in the pre-dawn when they were approaching the lek on foot, possibly hooting and displaying on the way. Goshawks, which have been reported to carry off full grown fowl, or wooden duck decoys (Bent, 1932), could no doubt also carry off an adult Sharp-tailed Grouse. The Great Horned Owl is also probably robust enough to carry a Sharp-tailed cock away, although this has never to my knowledge been documented. Berger et al. (1963) reported a Great Horned Owl carrying a Greater Prairie Chicken cock a short distance, although that particular owl was being pursued at the time by the observer.

In the autumn, a single example of possible raptor action on a lek was found in 1968. A large patch of feathers, almost certainly enough to indicate a successful kill, was found on a lek at that time, but no remains were found with them, hence the evidence for fall predation remains tentative.

Berger et al. (1963) found evidence for six raptor kills in 21 years of observation in Wisconsin. Although direct evidence for raptor kills was not obtained at Hodgson, the fact that four possible kills were found on leks during

the two year study suggest that raptor predation on leks may be somewhat heavier in Manitoba than in Wisconsin.

Mammals

According to Grange (1948), it is probable that predacious mammals often stalk grouse on their leks. Hamerstrom et al. (1965), however, in a comprehensive study of the effects of mammals on Prairie Chickens attending leks, recorded only one mammalian kill over a 21 year period which included 4,745 morning observations. This mammal kill, moreover, was by a domestic dog. In most cases the Prairie Chicken would not even flush if a Coyote (Canis latrans) or Fox (Vulpes fulva) crossed the lek. Hjorth (1968) found the Fox (Vulpes vulpes) to be almost harmless to Black Grouse on the lek.

Some evidence of mammalian predation on leks was found at Hodgson. On April 28, 1968, a Coyote was flushed from the edge of a lek that was active at the time. When I returned to the lek later in the day, I found the remains of a grouse which had probably been killed earlier that day. Since the corpse was broken up, with the remains scattered about, I concluded that it had at least been scavenged, if not killed, by a large mammalian predator, presumably the Coyote seen on the lek earlier in the day.

On May 4, 1969, another apparent mammalian kill was found. In this instance there were few feathers scattered,

and only the head and one wing were missing. The thoracic cavity had been eaten into through the neck. This kill was apparently the work of a mustelid predator, such as a weasel, which is known to consume avian prey in this manner (Urban, 1969).

Unknown Predators

One other successful kill was found on a lek during this study. In this case the evidence consisted of two large patches of grouse feathers including tail feathers and primaries. The grouse killed was a cock on the basis of the central retrices. The predator could not be identified.

Other Interspecific Interactions

Three other interspecific interactions, which did not involve predators, were observed, one with a Starling (Sturnus vulgaris), and two with Crows (Corvus brachyrhynchos).

The Starling was feeding in a field near an active lek with three cocks on it, when one of the cocks, tail-rattling and with head down, approached the Starling. When the cock was approximately three feet from it, the Starling flew off. This behavior, which appeared to represent a tendency for Sharp-tailed Grouse cocks to respond sexually or aggressively to an inappropriate stimulus, has been

reported in even more extreme form by Nero (1970) who observed a Sharp-tailed Grouse, on the center strip of the highway, displaying towards passing automobiles.

On one occasion, two Crows approached a single Sharp-tailed Grouse that was feeding at the edge of the road. The Grouse then flew off, and the Crows, after standing for a few minutes, also flew off. It is possible that the presence of the feeding grouse served to indicate to the Crows a possible food supply, and they therefore approached to investigate, but proof for this interpretation is lacking. On another occasion involving Crows, two Crows repeatedly harassed an active lek by flying at the cocks, or landing near them and hopping towards them. On no occasion did the cocks retaliate in any way, but consistently flushed away from the Crows.

Discussion

Because of the open situation of the lek and the conspicuous nature of the display, it might be expected that mortality due to predation would be particularly severe on the leks. Berger et al. (1963) and Koivisto (1965), however, suggested that the open situation of the lek, and the numbers of cocks attending it, would make the lek an unlikely place for predation to occur. In fact Berger et al. (1963) suggested that this protection afforded from predators may be one factor making an open lek area an ecological

requirement of the prairie grouse. As described below, indirect evidence based on estimates of mortality in my study and others, suggest that the lek is probably at worst a neutral, and possibly even an advantageous place for male Sharp-tailed Grouse to frequent.

Basing their estimates on returns from banded birds, Hamerstrom and Hamerstrom (1951) found the yearly mortality in male and female Sharp-tailed Grouse to be approximately 80%. Based on the life span of each of the 166 grouse in their sample, I calculated that the average life expectancy of the grouse which the Hamerstroms studied was about 1.24 years after full growth (Smith, 1966). Ammann (1957) estimated the average survival of full grown Sharp-tailed grouse to be 1.50 years. Ammann's estimation indicates an average yearly mortality among these grouse of about 64%, or about 16% lower than the comparable estimates of Hamerstrom and Hamerstrom (1951). For the male portion of his sample Ammann (1957) found an average life expectancy of 1.61 years, or an average yearly mortality of 62%, considerably lower than for the female portion of the sample.

At Hodgson, out of 16 males banded on leks in the spring of 1968, seven returned to their leks in the spring of 1969. The maximum yearly mortality among adult male Sharp-tailed Grouse from this sample was therefore approximately 56%. This figure, although based on a small sample,

agrees remarkably well with the percentage mortality found by Ammann (1957).

Evidence was obtained that five male Sharp-tailed Grouse died on leks, presumably due to predation, between June 20, 1968 and June 20, 1969. The number of cocks attending these leks during that time was 116. Using these figures, the yearly lek mortality computes to 4% of the individuals attending the lek. If the estimate (Berger et al., 1963) that a male Greater Prairie Chicken spends about one-tenth of its life on the lek is taken as the best estimate of the time spent on leks by male Sharp-tailed Grouse, and if mortality on the lek was the same as elsewhere, the expected mortality on the lek would be one-tenth of the yearly mortality, or 6.2% based on Ammann (1957), and 5.6% based on my own estimate of yearly mortality. The 4.3% figure actually obtained for lek mortality within a year was lower than either of these expected values. These results therefore favor the view, mentioned above, that with respect to mortality, the lek may be advantageous, and certainly not disadvantageous to the attending cocks.

GENERAL DISCUSSION

The Role of the Autumn Display

Among birds, the appearance, in autumn, of behavior similar to spring sexual displays occurs in a wide range of species (Morley, 1943). One function which has been suggested for these autumn displays (Nice, 1941; Watson, 1964), is that they may serve as a dispersing mechanism. The possibility that the autumn lek display of the Sharp-tailed Grouse may have a similar dispersing function was one hypothesis examined during this study. Several lines of evidence emerged which indicate that the autumn lek of the Sharp-tailed Grouse is involved in the dispersal of at least a part of the population, including both young and adult males. This evidence included observations of movements of individually color-marked adult males from one lek to another between spring and autumn, collections of juvenile males from autumn leks, and observations of movements of entire leks from one location to another. While not discounting the possibility that population shifts may also occur in the spring, these data present definite evidence that as in many other species, dispersal during the autumn also occurs in Sharp-tailed Grouse. The results suggest further, that as in the Red Grouse (Watson, 1964), such dispersal may constitute an important function of the fall display of this

species.

Since lek and territorial attachments, like other aspects of the display, are probably low in the fall, and as the manifestations of vegetative growth are greatest at that time, it seems that the fall display might be the time when dispersion of the population could be most easily effected. Since considerable recruitment occurs on active leks during the fall (Lumsden, 1965; Fig. 8), it is likely that where vegetation inhibits fall usage of a lek, it may fail to recruit juvenile and adult males. Should this reduced fall recruitment lead to reduced lek size during the next spring, it is entirely possible that over a period of years, the lek might disappear. Such a response to changing vegetation could tend to keep the population on a habitat in which the stage of succession from grassland to forest is optimum for the species. The observations at Hodgson are consistent with this view since all of the leks which were active in the fall were on short vegetation or ploughed fields. As well as functioning to disperse the grouse within their habitat, the return of the adult males to the autumn lek accompanied by strange adults and juvenile males, may provide an opportunity for redistribution of the males within the lek itself. During this study, evidence for such a redistribution of territories within the lek in the autumn was obtained (p. 41).

In a highly competitive mating system such as the lek, in which only a small proportion of the attending cocks actually fertilize any hens (Robel, 1967; Koivisto, 1965), mechanisms must exist which allow for reassortment in the lek hierarchy, so that younger or otherwise more able birds can replace formerly dominant reproductive cocks that die or relinquish their territories. By informing the juvenile males as to the location of the lek, and by serving to initiate them into the dominance hierarchy essential for success in this highly competitive mating system, the autumn lek provides conditions favoring this reassortment. To have at least some of the necessary reassortment of the lek hierarchy occur in the fall, as was found in this study, might be advantageous to the species by hastening the establishment of a stable, reproductively successful lek the next spring. In addition to functioning in dispersal and reassortment of the lek hierarchy, it is also probable that the fall display provides a desirable degree of continuity of territoriality and hierarchy between seasons for those cocks whose status on the lek does not change appreciably. Such continuity, provided by the reestablishment of previously held territories during the fall display, seems desirable because it might also tend to hasten the establishment of a stable lek the following spring.

In at least some avian species (Nice, 1941; Watson,

1964), it is known that both adult and juvenile males may establish territories in the fall to which they return during the following spring. Morley (1943) suggested that in songbirds such as the Song Sparrow (Melospiza melodia), this establishment of fall territories may impart to the owner the psychological advantage of ownership the next spring, a result that presumably would tend to enhance the tendency to utilize the same territory in successive seasons. From evidence found in this study (Appendix III), and that of Evans (1969), it is apparent that in Sharp-tailed Grouse, adult males may hold essentially the same territory in spring as they did the previous fall. Although no direct evidence was obtained, it also seems likely that at least some of the juvenile males that attend the fall display may establish territories that they return to in the next spring. Additional evidence for the hypothesis that the fall lek favors territorial continuity between seasons was provided by the findings that in almost all cases (26 out of 29), the cocks returned to the same lek in the fall as in the previous spring, and 5 out of 11 territories measured in the fall were essentially unchanged from their spring locations. The findings of this study thus support the dual hypotheses that autumn lek displays may be important in population dispersion, while simultaneously providing a necessary degree of continuity between years to allow an optimum sorting out of

dominance relations, and hence the establishment and maintenance of stable leks and optimum reproduction. Further questions concerning the autumn display which might profitably be examined on the basis of the above findings include the actual proportion and fate of juveniles that do not attend autumn leks, the relative success on spring leks of any cocks which fail to attend the fall lek, and the possibility that males move from large to smaller, or to new leks in times of high population levels, while moving from small to larger leks during low population levels.

Lek Organization

The data obtained in this study allowed a quantative approach to several comparative features of lek structure and organization. For example the characteristic of territory size was found to be influenced significantly by the position of the territory on the lek, peripheral territories being larger than those lying centrally within the lek. Also, increased vegetative cover on the lek resulted in larger territories, and hence apparently somewhat looser organization. The above observations, as well as evidence supporting the radiating lek hierarchy, and information showing that cocks interactions tend towards the center of the lek (Table VII), are discussed in more detail above (p. 92) in relation to the model of lek formation and maintenance.

It was apparent from analysis of territory maps in both 1968 and 1969 that the smaller leks on the study area (1 to 9 cocks) differed from the larger leks (10 or more) in at least two behavioral aspects; territory size and territorial stability. Smaller leks had significantly larger territories and apparently lower territorial stability than larger leks. Territorial stability was particularly low, and territory size particularly large on the two very small leks, containing one and three cocks respectively.

Hamerstrom and Hamerstrom (1955), found that small leks (1 to 10 cocks), and leks with more than 16 cocks showed lower reproductive efficiency than leks with 11 to 16 cocks. Although the causes of these differences were not determined, these authors drew attention to the less stable organization that appeared to be characteristic of the larger, less reproductively efficient leks. The "large" leks examined in this study almost entirely fall into the 10 to 16 cock category of Hamerstrom and Hamerstrom (1955), and therefore no comparison of territory size or stability could be made between leks with more than 16 cocks. Comparison with small leks, however, indicated a significant reduction in stability on small, compared to the "large" Sharp-tailed Grouse leks at Hodgson. Although direct evidence is lacking, these results suggest that as in the Greater Prairie Chicken studied by Hamerstrom and Hamerstrom

(1955), reproductive efficiency may have been reduced on the smaller leks. If so, the possibility that the observed differences in organization between large and small leks may be causative factors in this lower efficiency, indicates that further study in this area might prove enlightening.

Lek Predation

The biological significance of the various functions of the lek (Table I) would no doubt be enhanced if it were known that definite disadvantages due to higher predation also resulted from lek attendance. Some investigators (Lehmann, 1941; Hjorth, 1968), have suggested that predation on the lek could be a real threat to the male portion of the grouse population, while others (Berger et al., 1963; Koivisto, 1965) have expressed the opposite opinion, and have proposed that the lek affords a certain amount of protection from predators.

Berger et al. (1963), observed a maximum of 10 kills on Greater Prairie Chicken leks during 21 years of observation. The lek mortality for Sharp-tailed Grouse at Hodgson may have been considerably higher, with seven possible kills being found on 16 leks during only two years of observation.

Although the sample size from Hodgson was small, and several assumptions were made in the analysis (p. 112), the available evidence does suggest that, as in the Greater Prairie Chicken observed by Berger et al. (1963), the

mortality on the leks at Hodgson was probably lower than elsewhere on the home range of the attending cocks. These results then support the contention that, far from exposing the cocks to increased predation, the lek may actually function in providing an element of protection from predators during the spring and fall display period.

SUMMARY

The organization and functions of the spring and autumn lek of the Sharp-tailed Grouse were studied during the spring and autumn seasons of 1968 and 1969 near the town of Hodgson in the interlake region of Manitoba. The area studied was a mixture of cultivated lowlands, and aspen uplands including various stages of transition from open grassland to aspen forest.

To aid in the study, 85 cocks and 6 hens were trapped on 12 leks. The trapping equipment included cannon-nets, mist nets, and bownets. Each bird captured was sexed, weighed, aged, and individually marked with a leg band on each leg and a colored plastic neck band. Observations made on the leks included records of lek attendance by both males and hens, the times of arrival of the cocks on the lek, and the time that they spent there. In addition, the territories of banded cocks were recorded each day of observation by locating the grouse on the lek with reference to a marked grid, and recording these locations on a scale map of the grid.

The autumn lek display was observed briefly during 1967, and more intensively during the autumn seasons of 1968 and 1969. The earliest indications of lek activity in the fall were observed on September 12, 1968.

The intensity of lek activity appeared to increase as the autumn season progressed, until an apparent plateau

was reached in mid-October, after which it remained fairly constant until declining abruptly in mid-November. Despite this apparent increase in intensity of activity, it was found that the time spent on the leks actually decreased as the fall season progressed.

In comparing the fall display to the spring display, it was found that in autumn, the cocks arrived significantly later with respect to sunrise, and spent significantly less time on the lek than they did during the spring display. In addition, the intensity of the displays were apparently lower in autumn, with high intensity sounds such as "bottle popping" or "freezing" seldom observed. Mounted models which elicited repeated copulation in spring produced only mild alarm responses during the autumn display.

Several lines of evidence were uncovered which indicate that the autumn display may function in dispersal of at least some juvenile and adult males. This evidence included movements of adult cocks from small leks to large leks during the fall; the attendance of juvenile males at the fall display; and the movement of entire leks from one location to another during the autumn display period.

Some of the evidence obtained indicated that the increased vegetation cover in fall may in some cases stimulate the movement of leks, and thus dispersal of the population.

In addition to the evidence for dispersal during the fall display, evidence was also found that the fall display may serve as a time when some of the cocks redistribute themselves within the lek itself, while other cocks provide continuity by reestablishing their spring territories during the fall display. It seems that the occurrence of necessary dispersal and reestablishment during the non-reproductive fall display may hasten the establishment of efficient spring leks.

The earliest indications of spring lek attendance at Hodgson were observed on March 7, 1969. By the end of March 1969, the leks were regularly attended.

The number of cocks attending lek #2a during the spring of 1969 increased during the early part of the spring, reaching a peak by the last week of April, after which the numbers attending lek #2a, and the other leks studied remained stable or decreased slightly.

Evening lek attendance was observed during the spring seasons of 1968 and 1969, and it was found that the number of cocks attending was generally lower than in the morning display period.

By early June lek activity had decreased noticeably, and the latest lek attendance observed was on June 19, 1968.

The earliest recorded attendance of hens on the leks at Hodgson was at lek #2a on April 13, 1969. The peak

attendance of hens on lek #2a during 1969 was recorded on April 28, when 11 hens were counted. The last observed attendance of hens on leks at Hodgson was on June 11, 1969.

Times of arrivals of cocks on the lek were recorded during May and June of 1968, and from April to June in 1969. The average arrival time for both seasons was 54 minutes before sunrise. On lek #2a, it was found that the time that the cocks spent on the lek before sunrise increased during the first two weeks of April, and then remained stable until the leks were abandoned in June. It is submitted that the progressively earlier arrival times recorded in early April may correspond to the transition from arrival at sunrise to arrival at twilight which Hjorth (1968) recorded for the Black Grouse. Despite a decrease in activity on the lek, the cocks did not arrive later with respect to sunrise towards the end of the season, and it is suggested that this may be due to the fact that, as described by Hjorth (1968), the light intensity required to stimulate the cocks to display is available at earlier times during the later spring season as a result of the higher trajectory of the sun.

The springs of 1968 and 1969 were compared with regards to arrival times, and no significant differences were found to exist, despite the differing weather conditions between the two years. Arrival times on cloudy days

were compared to arrival times on clear days in both 1968 and 1969, and again no significant difference was found.

Arrival times on small leks were compared to arrival times on large leks, and it was found that no significant difference existed.

The time spent on the lek was found to increase during early spring, and then remain constant until the end of the season, despite the lower lek activity near the end of the season.

The time spent on the lek was compared between large and small leks, and between rainy and clear days, and no significant difference was found.

When the springs of 1968 and 1969 were compared for time spent on the lek, a significant difference was found to exist, with time spent on the lek being greater in 1969. It is suggested that this was due to the greater number of clear, dry days in 1969.

Precocious lek behavior was observed in a group of Sharp-tailed Grouse chicks of 3 and 4 days of age during June 1969.

Eighty-four territories were recorded during the study and examined with particular reference to lek organization.

The average territory size at Hodgson was $76m^2$, with the smallest territory being $3m^2$ and the largest being $715m^2$.

It was found that territories on small leks were significantly larger than those on large leks. In addition, it was apparent that at least in the case of very small leks (1 - 3 cocks), the territories were less stable than those on large leks. Despite this lower territorial stability of cocks on very small leks, one cock from a lek attended by only three males in 1968, returned alone to this lek in 1969, and displayed on the same territory which he had occupied during the previous spring.

Cocks holding territories near the center of the lek were predominately adult, and peripherally located cocks were predominately juvenile. It is submitted that this observation supports the argument that a radiating hierarchy exists on the lek. No correlation was found between position on the lek and body weight.

A peripheral cock on lek #2a was injected with testosterone in late May of 1969, and despite greatly increased activity by the injected cock, no change in territorial position was effected.

Territorial sizes were compared for central and peripheral cocks, and it was found that central territories were significantly smaller than peripheral ones.

Territory sizes on leks with tall vegetation were compared with territory sizes on leks with short vegetation and found to be significantly larger in area.

Territorial stability between early spring and late spring, and between seasons was compared with the aid of an index of territoriality derived for this purpose. It was found that territorial stability is greater in late spring than in early spring, and that stability within one spring season is greater than territorial stability between seasons.

The effect of moving immediate landmarks was found to have no apparent effect on the territorial stability of the cocks.

The direction of territorial interactions were found to be predominately towards the center of the lek. This tendency was more pronounced in peripheral cocks than in central cocks.

Four hypotheses of lek formation and maintenance were presented and evaluated, and seem consistent with the behavior exhibited by the grouse. On the basis of these hypotheses, territory size differences between large and small leks, central and peripheral cocks, and leks with heavy cover to leks with light cover are predicted. The attraction of the hens to the center of the lek is also explained on the basis of these hypotheses.

Seventeen avian, and two mammalian predators were observed near leks during 100 mornings of observation. Of these seventeen interactions between raptors and grouse,

four attacks were observed; two by Harriers, and one each by a Goshawk and a Great-Horned Owl. None of these attacks resulted in a kill. The reaction of the grouse appeared to depend on the species and behavior of the raptor.

Four instances of probable raptor predation, three cases of probable mammalian predation, and one instance where the predator was completely unknown were found on leks during the study. The amount of predation found on the leks at Hodgson, while greater than that observed for the Greater Prairie Chicken in Wisconsin (Berger et al., 1963), is still low enough to support the suggestion that one function of the lek may be protection from predators.

LITERATURE CITED

AMMANN, G. A. 1944. Determining the age of Pinnated and Sharp-tailed Grouse. J. Wildlife Management, 8: 170-171.

1957. The Prairie Grouse of Michigan. Game Div., Dept. Conservation, Lansing, Mich., 200 pp.

ANDERSON, R. K. and FRANCES HAMERSTROM. 1967. Hen decoys aid in trapping cock Prairie Chickens with bownets and noose carpets. J. Wildlife Management, 31: 829-832.

ANDERSON, R. K. 1969. Prairie Chicken responses to changing booming-ground cover type and height. J. Wildlife Management, 33: 636-643.

ANDREW, R. J. 1964. The development of adult responses from responses given during imprinting in the domestic chick. Anim. Beh. 12: 542-548.

ARMSTRONG, E. A. 1947. Bird display and behavior. An introduction to the study of bird psychology. Dover (1965). New York. 431 pp.

BAKER, M. F. 1953. Prairie chickens of Kansas. Univ. Kansas, Museum Nat. History Misc. Publ. 5, 68 pp.

BENT, A. C. 1932. (Dover, ed. 1963). Life histories of North American gallinaceous birds. U. S. Natl. Mus. Bull. 162, 490 pp.

BERGER, D. D., FRANCES HAMERSTROM, and F. N. HAMERSTROM. 1963. The effect of raptors on prairie chickens on booming-grounds. J. Wildlife Management, 27: 778-791.

BIRD, R. D. 1961. Ecology of the aspen parkland of western Canada in relation to land use. Research Branch, Canada Dept. of Agriculture Publication 1066. 155 pp.

BRECKENRIDGE, W. J. 1929. The booming of the prairie chicken. Auk, 46: 540-543.

BUDD, A. C. 1952. A key to the plants of the farming and ranching areas of the Canadian prairies. Experimental Farms Service, Dept. of Agriculture, Canada, 339 pp.

COCHRAN, W. G. 1953. Sampling techniques. J. Wiley and Sons Inc. New York. 413 pp.

DARLING, F. F. 1938. Bird flocks and the breeding cycle. Cambridge at the University Press. 124 pp.

DILL, H. H. and W. H. THORNSBERRY. 1950. A cannon projected net-trap for capturing water fowl. J. Wildlife Management, 14: 132-137.

EMLEN, J. T. Jr. 1952. Flocking behavior in birds. Auk, 69: 160-170.

ENG, R. L. 1961. Sage Grouse. Spring strutting activity. Nature, 11: 15-20.

1963. Observations on the breeding biology of the male Sage Grouse. J. Wildlife Management, 27: 841-846.

EVANS, R. M. 1960. Determining the age of Sharp-tailed Grouse by techniques based on feather characters (Unpublished).

1961. Courtship and mating behavior of Sharp-tailed Grouse (Pedioecetes phasianellus jamsei, Lincoln). Unpubl. M.Sc. thesis, Univ. Alberta. 134 pp.

1968. Early aggressive responses in domestic chicks. Anim. Behav., 16: 24-28.

1969. Territorial stability in Sharp-tailed Grouse. Wilson Bull., 81: 75-78.

FABRICIUS, E. 1962. Some aspects of imprinting in birds. Symp. Zool. Soc. London, No. 8: 139-148.

FRANKTON, C. 1956. Weeds of Canada. Can. Dept. of Agriculture, Botany and Plant Pathology Div. Sci. Service. Ottawa, Ont.

FREUND, J. E. 1960. Modern elementary statistics. Prentice-Hall Inc. Englewood Cliffs, N.J. 432 pp.

GOWER, C. W. 1939. The use of the bursa of Fabricius as an indication of age in game birds. Trans. Fourth N. Amer. Wildlife Conf.: 426-430.

GRANGE, W. B. 1948. Wisconsin grouse problems. Wisconsin Cons. Dept., Publ. 328, Madison, Wisconsin. 318 pp.

GRIFFIN, D. R. and A. NOVICK. 1962. Animal structure and function. Second Ed. Modern Biology Series, Holt, Rinehart and Winston Inc. 231 pp.

HAMERSTROM, F. N. Jr. 1939. A study of Wisconsin Prairie Chicken and Sharp-tailed Grouse. Wilson Bull. 51: 105-120.

1942. Progress report No. 5, 1940-1941. Prairie Grouse Cooperative, University of Michigan. Piackney, Michigan.

HAMERSTROM, F. N. Jr., and F. HAMERSTROM. 1951. Mobility of the Sharp-tailed Grouse in relation to its ecology and distribution. Amer. Midl. Nat., 46: 174-226.

1955. Population density and behavior in Wisconsin Prairie Chickens (Tympanuchus cupido pinnatus). Int. Ornithol. Congr. Basil. 9: 459-466.

1960. Comparability of some social displays of grouse. Proc. XII Intern. Ornithol. Congr., Helsinki: 274-293.

HAMERSTROM, FRANCES, D. D. BERGER, and F. N. HAMERSTROM Jr. 1965. The effect of mammals on prairie chickens on booming grounds. J. Wildlife Management, 29: 536-542.

HART, C. M., O. S. LEE, and J. B. LOW. 1950. The Sharp-tailed Grouse in Utah. Utah Dept. Fish and Game, Publ. 3, 79 pp.

HENDERSON, F., F. W. BROOKS, R. E. WOOD, and R. B. DAHLGREN. 1967. Sexing of prairie grouse by crown feather pattern. J. Wildlife Management 31: 764-769.

HJORTH, I. 1966. Arena display of the Black Grouse (Lyrurus tetrix tetrix). Phil. Trans. Royal Soc., London. 251: 485-492.

1968. Significance of light in the initiation of morning display of the Black Grouse (Lyrurus tetrix tetrix). Viltrevy, 5: 39-94.

HOHN, E. O. 1953. Display and mating behavior of the Black Grouse (Lyrurus tetrix, L.). Brit. J. Anim. Beh. 1: 48-58.

HUTCHINSON, G. E. 1957. A treatise on limnology. Vol. 1, Wiley and Sons, New York. 1015 pp.

HUXLEY, J. S. 1934. A natural experiment on the territorial instinct. Brit. Birds. 47: 270-277.

KOIVISTO, I. 1965. Behavior of the Black Grouse (Lyrurus tetrix L.) during the spring display. Pap. Finnish Game Res. No. 26.

KRUIJT, J. P. and J. A. HOGAN. 1967. Social behavior on the lek in Black Grouse (Lyrurus tetrix tetrix L.). Ardea 55: 203-240.

LACK, D. 1939. The display of the Blackcock. Brit. Birds 32: 290-303.

1968. Ecological adoptions for breeding in birds. Methuen and Co. Ltd., London.

LEHMANN, V. W. 1941. Attwater's Prairie Chicken, its life history and management. North Amer. Fauna, 57: 1-65.

LUMSDEN, H. G. 1965. Displays of the Sharp-tailed Grouse. Ontario Dept. Lands and Forests, Report No. 66. 68 pp.

1968. The displays of the Sage Grouse. Ontario Dept. Lands and Forests, Report No. 83. 94 pp.

~~MAYR, E. 1963. Animal species and evolution. Belknap Press, Cambridge, Mass. 797 pp.~~

MILLER, H. W. 1957. A modified cannon for use on the projected net trap. Nebraska Game, Forestation and Parks Commission. 6 pp.

MORLEY, A. 1943. Sexual behavior in British birds from October to January. Ibis. 85: 132-157.

NERO, R. W. 1970. Sharp-tailed Grouse gives aggressive display to automobiles. Wilson Bull. 82: 221-222.

NICE, M. N. 1941. The role of territory in bird life. Am. Midland Naturalist, 26: 441-487.

NITCHUK, W. M. 1969. Histological changes in the testes of the Sharp-tailed Grouse (Pedioecetes phasianellus Linnaeus) in relation to dancing ground size and organization. Unpubl. M.Sc. thesis, Univ. Manitoba. 113 pp.

PETERLE, T. J. 1954. The Sharp-tailed Grouse in the Upper Penninsula of Michigan. Ph.D. thesis, Univ. Michigan. 275 pp. Univ. Microfilms. Ann Arbor, Mich.

1956. Trapping techniques and banding returns for Michigan Sharp-tailed Grouse. J. Wildlife Management 20: 50-55.

RIPPIN, A. B. 1970. Social organization and recruitment on the arena of Sharp-tailed Grouse. Unpubl. M.Sc. thesis, Univ. of Alberta. 59 pp.

ROBEL, R. J. 1965. Quantitative indices to activity and territoriality of booming Tympanuchus cupido pinnatus in Kansas. Trans. Kansas Acad. Sci., 67: 702-712.

1967. Significance of booming grounds of Greater Prairie Chickens. Proc. Amer. Philos. Soc. 111: 109-114.

1969. Movements and flock stratification within a population of Blackcocks in Scotland. J. Anim. Ecol. 38: 755-763.

1970. Possible role of behavior in regulating Greater Prairie Chicken populations. J. Wildlife Management, 34: 306-312.

SCHWARTZ, C. W. 1945. The ecology of the Prairie Chicken in Missouri. Univ. of Missouri Studies, 20: 1-99.

SCOTT, J. W. 1942. Mating behavior of the Sage Grouse. Auk, 59: 477-498.

1950. A study of the phylogenetic or comparative behavior of three species of Grouse. Ann. N.Y. Acad. Sci. 51: 1062-1073.

SETON, E. T. 1940. Trail of an artist naturalist. Charles Schribner's Sons, N.Y. 412 pp.

SIEGEL, S. 1956. Non parametric statistics for the behavioral sciences. McGraw-Hill Book Co. Ltd. 312 pp.

SIMON, J. R. 1940. Mating performance of the Sage Grouse. Auk, 57: 467-471.

SMITH, R. L. 1966. Ecology and field biology. Harper and Row. N.Y., London. 686 pp.

SNYDER, L. L. 1935. A study of the Sharp-tailed Grouse. Univ. Toronto Press. 166 pp.

STEARN, C. W. 1956. Stratigraphy and paleontology of the Interlake Group and Stonewall Formation of southern Manitoba. Canada, Geological Survey. Memoir 281.

TINBERGEN, N. 1939. The behavior of the Snow Bunting in spring. Trans. Linnaean Soc. N.Y. 5: 1-95.

URBAN, R. E. 1969. Food habits of mink in the Turtle Mountain area of Manitoba. Unpubl. M.Sc. thesis, Univ. Manitoba. 119 pp.

WATSON, A. 1964. Aggression and population regulation in Red Grouse. Nature, 202: 506-507.

~~1965. A population study of Ptarmigan (Lagopus mutus) in Scotland. J. Anim. Ecol. 34: 135-172.~~

WATSON, A. and D. JENKINS. 1964. Notes on the behaviour of the Red Grouse. Brit. Birds, 57: 137-170.

WRIGHT, P. L. and R. W. HIATT. 1943. Outer primaries as age determiners in gallinaceous birds. Auk, 60: 265-266.

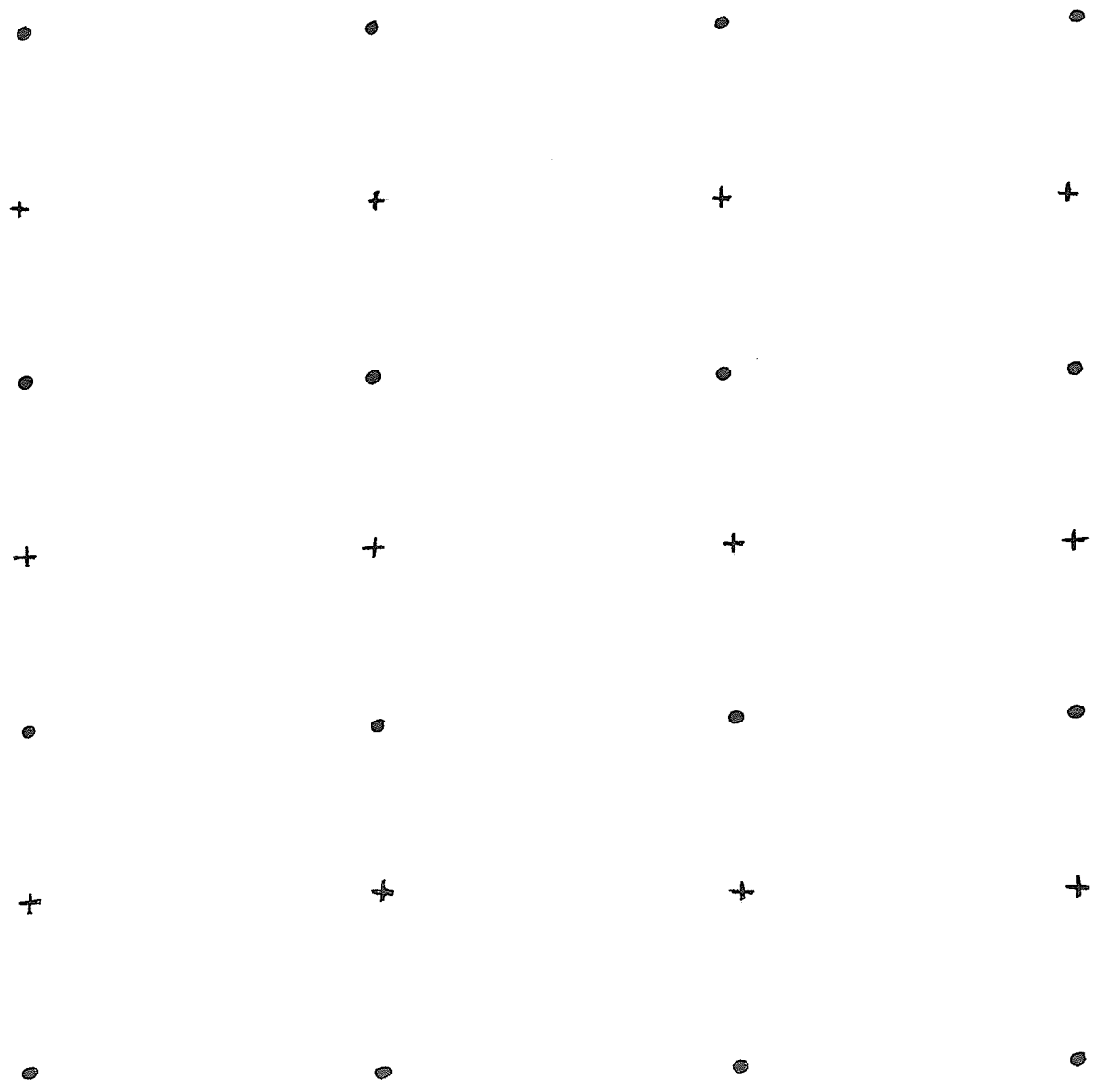
WYNNE-EDWARDS, V. C. 1962. Animal dispersion in relation to social behavior. Hafner, New York. 653 pp.

APPENDIX I

Sample of scale replica of lek grid on which territories were recorded

Date _____

Lek _____



Time _____

APPENDIX II

Sample of data sheet used to record information on Sharp-tailed Grouse leks

DATA SHEET

DATE _____

D.G. _____

MY ARRIVAL TIME _____

TEMP. _____

VISIBILITY _____

PRECIPITATION _____

CLOUD CONDITIONS _____

WIND: Direction _____

Velocity _____

TIME OF FIRST INDICATION OF GROUSE _____

TIME OF 1ST GROUSE ON D.G. _____

MAXIMUM # PRESENT _____

HOURLY COUNTS:

1) _____ 2) _____

3) _____ 4) _____

5) _____ 6) _____

BANDED BIRDS PRESENT:

_____

_____

_____

_____

_____

TIME OF DEPARTURE OF 1ST CENTRAL BIRD _____

TIME OF DEPARTURE OF LAST BIRD _____

GENERAL OBSERVATIONS

COPULATIONS: _____

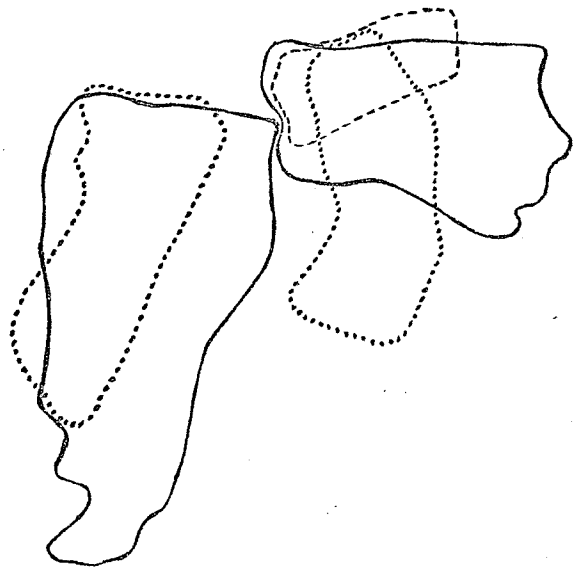
HENS PRESENT _____

DIRECTION OF: Arrival _____

Departure _____

APPENDIX III

Maps showing the territories of two cocks on lek number 17 during the spring of 1968, fall of 1968, and spring of 1969



——— SPRING 1968

------ FALL 1968

..... SPRING 1969