5-1-1971

Acoustical Communication in the Sharp-Tailed Grouse

Louis Henry Kermott III

Recommended Citation

Kermott, Louis Henry III, "Acoustical Communication in the Sharp-Tailed Grouse" (1971). *Theses and Dissertations*. 3495.
https://commons.und.edu/theses/3495

ACOUSTICAL COMMUNICATION IN THE SHARP-TAILED GROUSE

by
Louis Henry Kermott III

Bachelor of Science, University of North Dakota 1962

A Thesis

Submitted to the Faculty

of the

University of North Dakota

in partial fulfillment of the requirements

for the degree of

Master of Science

Grand Forks, North Dakota

May
1971

[redacted]

This Thesis submitted by Louis Henry Kermott III in partial fulfillment of the requirements for the Degree of Master of Science from the University of North Dakota is hereby approved by the Faculty Advisory Committee under whom the work has been done.

Lewis W. Oring
(Chairman)

Paul B. Kannowski

A William Johnson
Dean of the Graduate School

[redacted]

Permission

Title Acoustical Communication in the Sharp-tailed Grouse

Department Biology

Degree Master of Science

In presenting this thesis in partial fulfillment of the requirements for a graduate degree from the University of North Dakota, I agree that the Library of this University shall make it freely available for inspection. I further agree that permission for extensive copying for scholarly purposes may be granted by the professor who supervised my thesis work or, in his absence, by the Chairman of the Department or the Dean of the Graduate School. It is understood that any copying or publication or other use of this thesis or part thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of North Dakota in any scholarly use which may be made of any material in my thesis.

Signature L. Henry Kermott

Date April 27, 1971

ACKNOWLEDGEMENTS

I wish to thank L. W. Oring for guidance and help throughout the course of my study. P. B. Kannowski and M. K. Wali made suggestions regarding the manuscript. R. J. Trobec helped in the capture and marking of birds, G. P. Icenogle in the collecting of data, and K. B. Modahl in the making of spectrograms. Special thanks are due my wife, Cathy, for patience and typing of the preliminary manuscript. This study was supported by two grants from the University of North Dakota Biology Department and a Louis Agassiz Fuertes grant of the Wilson Ornithological Society.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

ABSTRACT

The Sharp-tailed Grouse has evolved a highly complex system of visual and acoustical signals due to increased social interactions necessary with the predator pressure of an exposed environment. The first portion of the spring mating season is primarily involved with establishment and defense of territories. Predominant acoustical signals are aggressive, highly ritualized, and involved in individual location and recognition. During mid-season females visit the lek, are courted by males, and copulations occur. Acoustical signals are concerned with attracting and stimulating females, vary on a time and frequency continuum, and are thus not as highly ritualized. During the last portion of the season activity tapers off and acoustical signals diminish.

INTRODUCTION

The Sharp-tailed Grouse (Pedioecetes phasianellus) is one of a number of grouse species possessing traditional, communal display grounds. Early on spring mornings, males gather on these "dancing" grounds or leks, establish territories, and engage in displays. Females visit the lek, are courted by males, and fertilized. They then leave, establish nests, and raise young alone.

Most studies of grouse have been management oriented, dealing largely with habitat utilization, movements, etc. (see Evans, 1968, for a general review of grouse literature). Detailed behavioral analyses exist for several species, especially the Black Grouse (Lyrurus tetrix) (Kruijt and Hogan, 1967; Höhn, 1953) and Greater Prairie Chicken (Tympanuchus cupido) (Hamerstrom and Hamerstrom, 1960; Robel, 1965, 1966, 1967). Displays of the Sharp-tailed Grouse have been described in considerable detail by Evans (1961) and Lumsden (1965).

Sharp-tails produce a variety of loud and frequent sounds. Evans (1961) briefly described the sounds; Lumsden (1965) described them and proposed hypothetical functions. Neither author gathered systematic or detailed data on acoustical behavior.

On the basis of a pilot study in 1969, it appeared that the quality and quantity of sounds made by males on the lek changed with different parts of the mating season; that the various sounds varied slightly between individuals; that individual recognition by sound alone occurred allowing identification of neighbors and strangers; and that some sounds were highly ritualized, stereotyped, and related to aggression, while others were less so and concerned with attraction and stimulation of females.

With these hypotheses in mind a study of lek acoustical behavior was undertaken in 1970. Attempts were made to: 1) describe and classify vocalizations and other acoustical behavior quantitatively, paying special attention to differences between individuals; 2) document changes in the nature of sound communication by males through the season; 3) relate acoustical communication to other forms of behavior; 4) discern the adaptive significance and function of behavior; and 5) gain insight into the evolution of lek behavior.

METHODS

Observations were made from blinds set up on two leks: one was studied intensively and used for experimental work, the other served as a control ground and was disturbed as little as possible. The experimental lek was located on grassland nine miles west of Grand Forks, Section 19, T151N R51W Grand Forks County, North Dakota. At one time the area was heavily grazed but it has not been used for agricultural purposes for at least five years. The control ground, seven miles directly north of the experimental ground, was located in a hay meadow.

The experimental lek was visited every morning from late March until early July--weather permitting--from two hours before sunrise until all birds left for the morning. A very wet spring limited the number of mornings that visits could be made, yet 44 complete mornings were spent in the blind. The control lek was visited on three mornings.

Seven territorial males were captured using a Miller cannon projected net. They were then marked with colored numbered leg bands and/or enamel paint on top of the head (Table 1). The lek was marked with a grid of numbered stakes at three meter intervals around the periphery, and six

TABLE 1

KEY TO INDIVIDUALLY IDENTIFIABLE BIRDS[a]

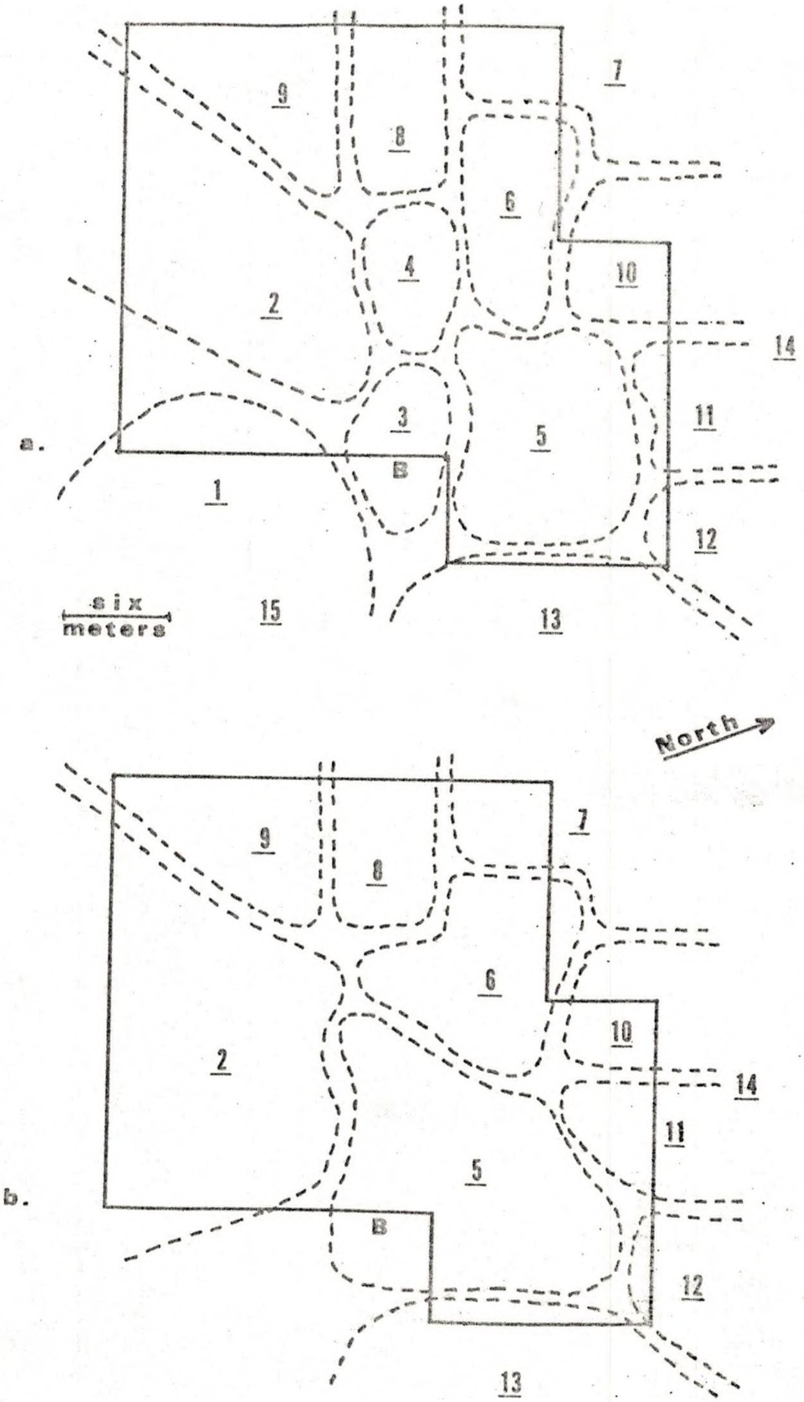
Bird Number	Leg Band	Head Color	Sex	Date Marked
1	Yellow, 141	Yellow	Male	3 May 1970
2	Blue, 93	Blue	Male	3 May 1970
3	Yellow, 40	None	Male	14 May 1969
4	Green, 7	Green	Male	3 May 1970
5	Red, 77	Yellow	Male	2 May 1970
8	Green, 11	Blue	Male	3 May 1970
10	Yellow, 142	Black	Male	3 May 1970
--	Red, 100	Red	Female	3 May 1970

[a] Birds marked in 1969, but not present in 1970, are not included.

meter intervals through the center (after Evans, 1961, and Trobec, 1970). Territories were determined easily and precisely by marking the location of each face-off on a map corresponding to the lek grid (see maps, Figure 1).

Entire morning recordings were made at intervals throughout the season with a Sony F 121 microphone placed on the lek and connected to a Uher 4000R-L tape recorder in the blind. These tapes were replayed later at reduced speed and all coos, gobbles, dances, and chilks counted using a multiple tally counter. During heights of activity, males at the far side of the lek were difficult to hear above the sounds made by males closer to the microphone, and may not have been counted. Since microphone placement remained constant from day to day, experimental error should be consistent in this respect.

Four selected males (birds 2, 3, 4, and 5) were intensively studied at approximately weekly intervals by recording their total activity, minute by minute, for two one-half hour periods, using a stopwatch and note pad. All activities and conditions on the lek influencing the male were noted, including presence of females. The times of the two periods of observation were standardized. The first always began as soon as it was light enough to identify individuals and to see the note pad. This usually occurred about 15 to 30 minutes after initial arrival of the birds. Activity was noted for one-half hour; one hour later the second one-half hour period began. The same birds were recorded at similar intervals


a.
9
8
7
6
4
10
2
14
3
11
5
B
1
12
six meters
15
13
North
b.
9
8
7
6
10
2
14
11
5
B
12
13

using a unidirectional microphone (Electro-Voice 644) from the blind, with identification of each bird made by speaking into the rear of the microphone. Sound spectrograms were made playing tapes on Uher 4000R-L recorders at normal speed into a Kay Electric Company Sonagraph, model 7029A, at wide and narrow band settings.

Experimental tapes of coos, gobbles, dances with chilks, and face-off chatter were played on the experimental lek through a small (3 x 5 inch) speaker placed in a standard location in bird 5's territory, at times representing early (12-23 April), mid (11-21 May), and late (1-11 June) season. Tapes were made from recordings taken from the same lek the previous year and consisted of two-minute segments of each sound. It should be noted that of the males present on the lek the first season only one was present the second. In effect, then, the second season's birds represented a different population. Each sound segment was played on a separate day and repeated five times. Tapes were not played during periods of activity, but only when all birds had been quiet for 10 minutes. Initial reactions and elapsed time to these reactions were noted, as well as subsequent reactions. Only rough quantification of reactions was attempted. Stuffed models of grouse were not used.

DESCRIPTIONS OF ACOUSTICAL BEHAVIOR

Sound terminology below is that used by Lumsden (1965), except for sounds given during boundary disputes referred to here as face-off whine and chatter. Lumsden described but did not name these sounds. Measurements were made from spectrograms: frequency using narrow band setting, time using wide band setting. Any analysis of this type is somewhat subjective, and frequency measurements in particular represent average values.

Coo. This vocalization is part of the cooing display. The body is tilted forward and downward with neck extended, bill pointed downward, tail closed and held horizontal or pointed slightly upward, and crest raised. The sound is produced as the head and neck pump slightly downward and cervical apteria bulge outward. Coos are frequently repeated in long series of 20 to 30 in one to two minutes.

Examination of a spectrogram reveals a single note beginning around 350 Hz and sliding downward to 300 Hz, duration averaging 0.16 second (Figure 2a). Overtones may or may not be present, and may be related to direction bird is facing, distance from microphone, or recording levels of recorder or Sonagraph.

Table 2 presents numerical descriptions of coos from random samples of the population and from four intensively studied males. Two figures are given for frequency, initial and final. Individuals were not highly variable with regard to frequency. In the case of birds 3 and 4 it was not possible to measure any variability in the frequency of their respective coos, and thus the standard deviation was given as zero. A *t* test revealed no significant difference in frequency between birds 2 and 5.

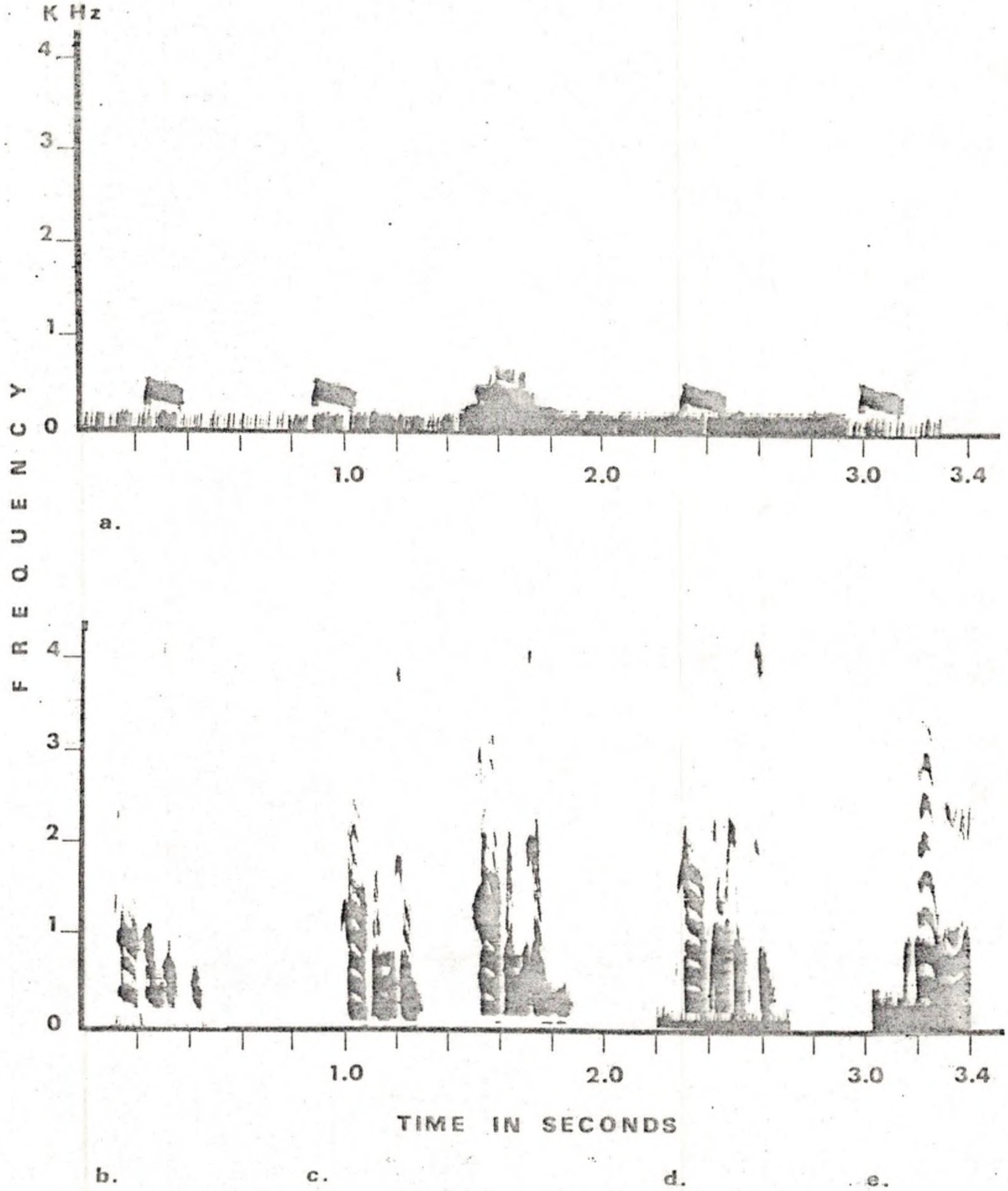

K Hz
4
3
2
1
0
FREQUENCY
1.0
2.0
3.0
3.4
a.
4
3
2
1
0
1.0
2.0
3.0
3.4
TIME IN SECONDS
b.
c.
d.
e.

TABLE 2

NUMERICAL DESCRIPTIONS OF <u>COOS</u> FROM RANDOM SAMPLES OF THE POPULATION AND FROM FOUR INTENSIVELY STUDIED MALES (frequencies in Hz; time in seconds; N = sample size; $\overline{X}$ = mean; S.D. = standard deviation)

	N	$\overline{X}$	S.D.
Random Sample			
Initial Frequency	80	339	36
Final Frequency	80	299	32
Duration	80	0.230	0.051
Bird <u>2</u>			
Initial Frequency	19	329	25
Final Frequency	19	290	36
Duration	19	0.243	0.055
Bird <u>3</u>			
Initial Frequency	6	400	0
Final Frequency	6	350	0
Duration	6	0.24	0.020
Bird <u>4</u>			
Initial Frequency	13	350	0
Final Frequency	13	300	0
Duration	13	0.185	0.020
Bird <u>5</u>			
Initial Frequency	15	317	41
Final Frequency	15	290	28
Duration	15	0.266	0.066

Duration of <u>coos</u> showed great variability in the population and in individuals. Among the four individuals sampled, analysis of variance showed bird <u>4</u> to be significantly different in <u>coo</u> duration ($F = 6.39$, for three and 49 degrees of freedom, $p < 0.01$). Since only four males were sampled, it is possible that further sampling might have resulted in no significant difference. No significant differences in coo frequency or duration were found at different times of the season for these individuals.

Gobble. No ritualized visual display is associated with the gobble. Most commonly it is given from the upright alert posture, but may be given from the cooing or dancing posture. It is a vocalization.

Examination of a spectrogram of bird 2 shows the gobble to be complex, composed of four basic syllables or notes, each preceded by a short upward stroke (Figure 2b). Table 3 provides a numerical description of this gobble. Spectrum indicates the frequencies where most energy is concentrated in each note. Total interval duration is the time from one note to the next. It should be kept in mind that the stroke preceding the next note begins midway through this interval.

Analyses of five other gobbles of bird 2 from different parts of the season showed no measurable deviation from Table 3.

Figure 2c is a spectrogram of two gobbles of bird 3. No measurable differences exist in the first or second notes or in the intervening interval. The interval preceding the third note, however, is slightly narrower in the second gobble (range, 0.02 to 0.04 second, N = 11) and the third note slightly longer (range, 0.08 to 0.14 second, N = 11), leading to variability in total duration of gobbles from this bird, but not frequencies. Compared with bird 2 it appears that the third and fourth notes have been condensed into a single slurred note of variable duration.

TABLE 3

NUMERICAL ANALYSIS OF A SINGLE *GOBBLE* FROM BIRD *2*
(spectrum = frequencies containing most sound
energy in Hz; time in seconds)

Preliminary stroke duration			.02
Note 1:	spectrum	300,600,900	
	duration		.06
Interval:	total duration		.04
	stroke duration		.02
Note 2:	spectrum	300,600,900	
	duration		.06
Interval:	total duration		.02
	stroke duration		.02
Note 3:	spectrum	300,600	
	duration		.04
Interval:	total duration		.06
	stroke duration		.04
Note 4:	spectrum	300	
	duration		.04
Total duration of *gobble*			.34

Nine more *gobbles* from this bird from different parts of the season were consistent in number of notes (three) and in frequency spectrum and durations through the second note, but differed as described above.

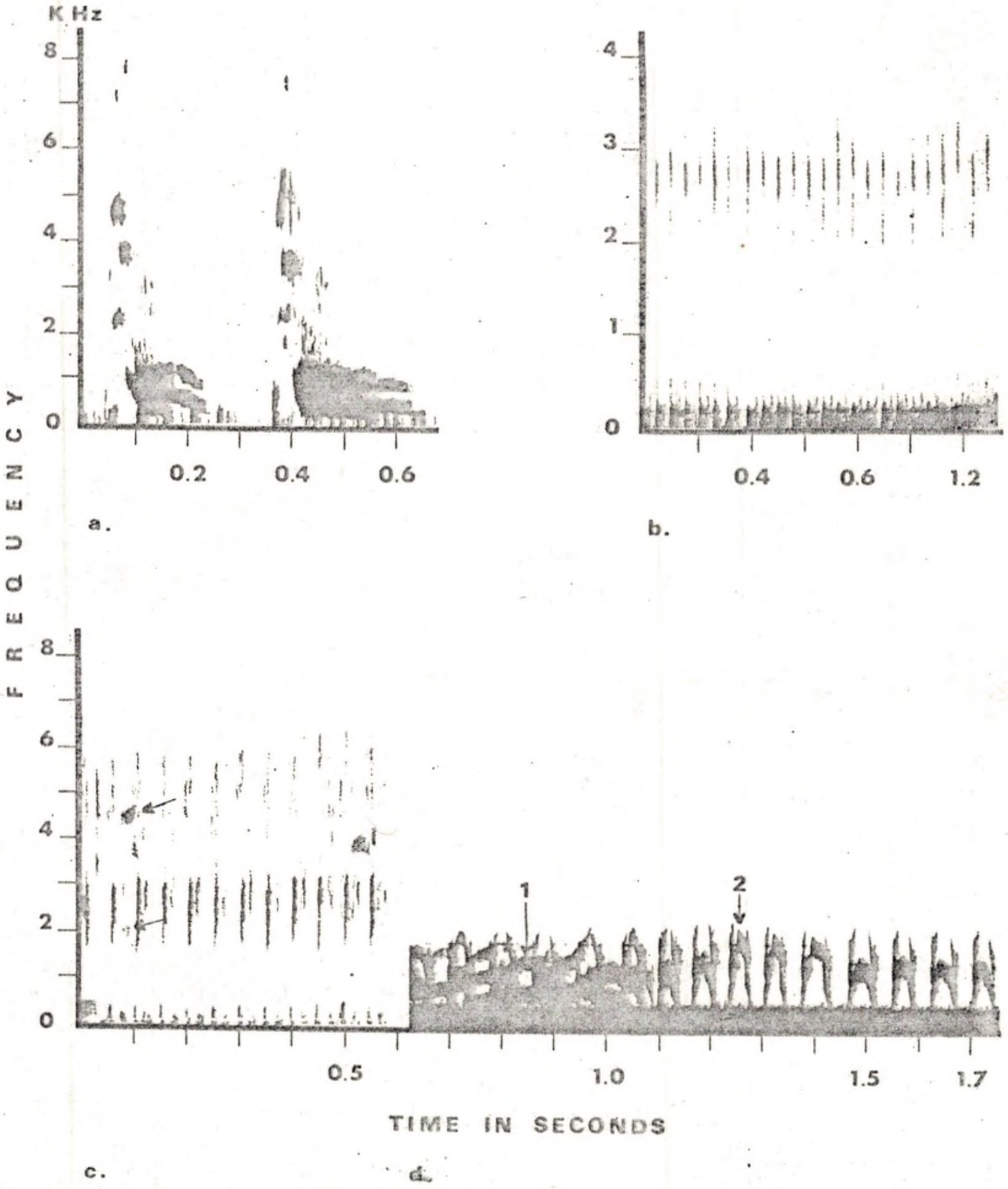
A spectrogram of a *gobble* of bird *5* showed four notes (Figure 2d). Five samples taken from the first half of the season were identical. Five samples taken late in the year were identical except for a consistent 0.02 second elongation of the fourth note.

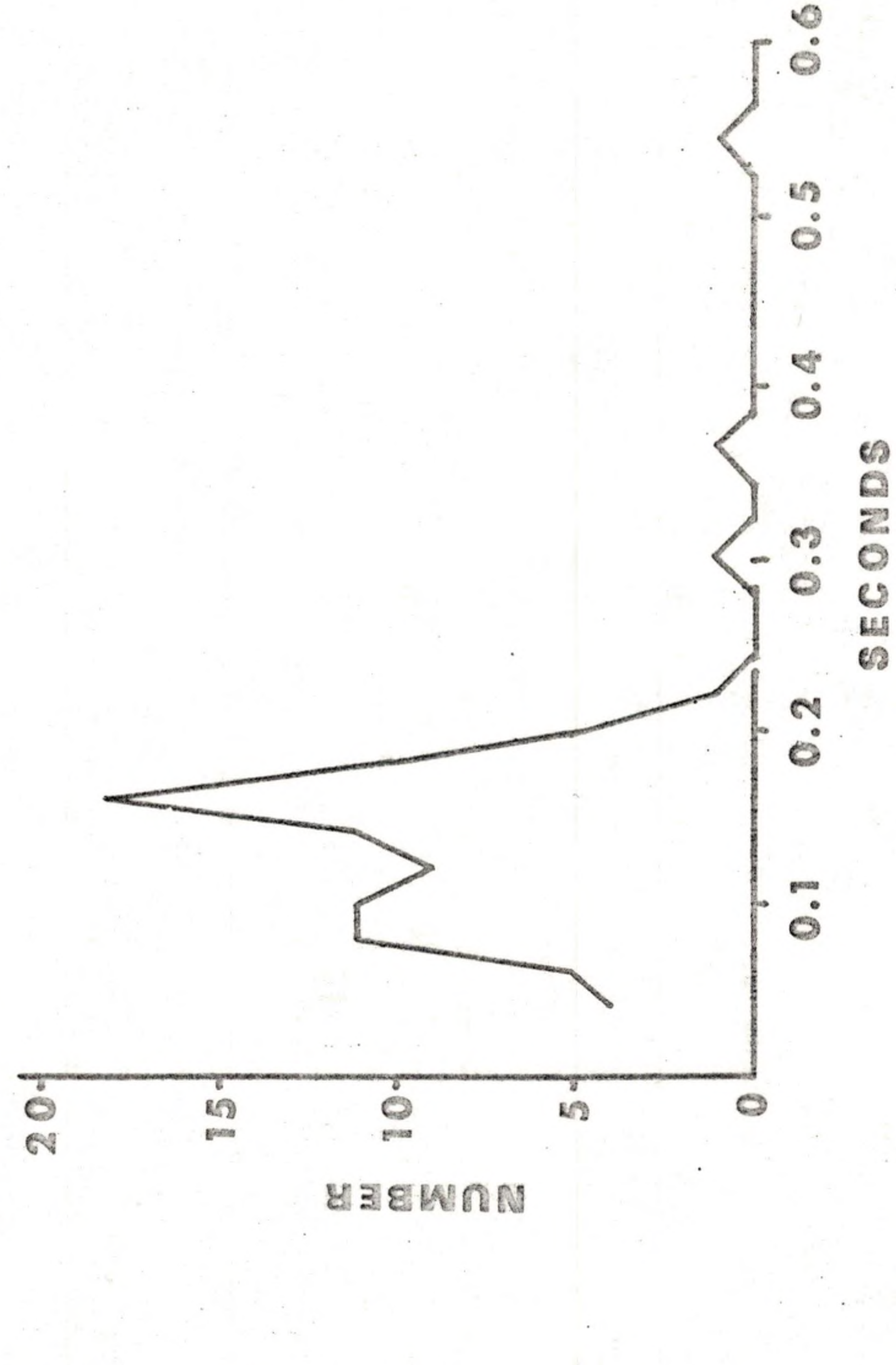
Chilk and Cha. These vocalizations were not directly related to a corresponding visual display. They were given at any time from the upright alert or any display posture. When a display was interrupted by a chilk, the bird frequently resumed the display.

Spectrograms of two chilks, selected randomly, are shown in Figure 3a. Each consists of two notes: the first an upward stroke ending with energy concentrated in three tones; the second a drawn out note with energy at low frequency levels. Both vocalizations are very similar, the primary difference being the length of the second note, with the second chilk having a longer total duration due to a more drawn out second note.

Although described by some authors as separate vocalizations, the chilk and cha represent end points of a time continuum. A random sampling of all parts of the season gave durations ranging from 0.04 to 0.54 second, with mean value of 0.146 second, and standard deviation of 0.081 second (N = 88). Examination of Figure 4 shows a fairly normal distribution with a few vocalizations of considerably longer duration. Formerly, those of long duration would have been called chas. I recommend dropping this term and using the term chilk exclusively.

Analyses of 20 chilks of birds 2 and 5 representing early and late season failed to reveal any consistent differences or similarities except for the two notes as described. Due to the obvious complexity of this


K Hz
8
6
4
2
0
FREQUENCY
0.2
0.4
0.6
a.
4
3
2
1
0
0.4
0.6
1.2
b.
8
6
4
2
0
1
2
0.5
1.0
1.5
1.7
TIME IN SECONDS
c.
d.


NUMBER
0
5
10
15
20
SECONDS
0.1
0.2
0.3
0.4
0.5
0.6

vocalization I have not given any numerical description other than that above.

Tail-rattling. This is the only sound made by Sharp-tails on the lek that is not a vocalization. A rapid series of clicks is produced by lateral movement of the tail causing the rectrices to scrape across one another (see Lumsden, 1965, for anatomical discussion). Tail-rattling is part of the dancing display, but since the two are inseparable I have used the terms interchangeably.

A spectrogram shows energy concentrated in two frequency ranges: a low component around 200 Hz, and a high one from 3000 to 3500 Hz (Figure 3b). Analysis of a random selection is given in Table 4. I have not analyzed the low component due to difficulty in measuring low frequencies precisely, however it never exceeds 400 Hz.

Analysis of click rates indicated males danced at a faster rate late in the season than early ($t = 8.26$ for 50 degrees of freedom, $p < 0.01$), and at a faster rate when females were present (comparing 25 April vs. 26 April, $t = 6.17$ for 38 degrees of freedom, $p < 0.01$) (Table 4). Comparing 26 April with 2 June ($t = 3.3$ for 50 degrees of freedom, $p < 0.01$) indicated that the late season rate was significantly greater with no females present than mid-season with females present.

Individual males appeared to dance at slightly different but consistent rates on a given morning. On 2 June, bird 2 consistently danced

TABLE 4

NUMERICAL DESCRIPTION OF DANCING (N = sample size; $\overline{X}$ = mean; S.D. = standard deviation)

		N	$\overline{X}$	S.D.
Tail-rattling; random sample				
Frequency in Hz	High	12	3280	200
	Low	Less than 400 (see text)		
Clicks/sec.; random sample				
18 April; females absent		20	18.20	0.74
25 April; females absent		20	18.20	0.63
26 April; females present		20	19.44	0.64
2 June; females absent		20	20.20	0.91
Clicks/sec.; Bird 2				
2 June		5	20.0	0.0
Clicks/sec.; Bird 5				
2 June		6	19.2	0.0
Dance sequence length in seconds; random sample				
14 April; females absent		20	2.45	1.49
25 April; females absent		20	2.45	1.31
26 April; females present		20	5.25	1.14
19 May; females absent		20	3.43	2.17

at a slightly greater rate than bird 5 (Table 4). Unfortunately, I have no further data on individual rates.

All above data on click rates were taken by slowing tapes to one-eighth normal speed and counting for 20 seconds. Data taken from spectrograms were similar.

Length of individual *dance* sequences varied depending upon the time of the season and the presence or absence of females (Table 4). Analysis of variance indicated the differences were highly significant ($F = 74$, for three and 76 degrees of freedom, $P < 0.01$). A Keuls multiple range test further showed length of *dances* greater late in the season than early (P 0.05), and much greater when females were present (P 0.01), compared with any time when females were not present.

Pow call. This vocalization, the *pow*, which sounds like pulling a cork from a bottle, was given only during the *dancing* display. However, it did not accompany every *dance* sequence. The percent of *dance* sequences accompanied by one or more *pows* was higher later in the season and much higher when females were present (Table 5).

Figure 3c is a spectrogram of a *dancing* sequence with associated *pows* shown at the arrows. Numerical analysis of a random sampling is shown in Table 5.

Face-off whine and chatter. When two males meet at a territorial boundary and engage in a ritualized aggressive display it is accompanied by a vocalization which may vary from a *whine* to a staccato *chatter*. Both males take part and the sounds are loudest when aggressive motivation appears greatest. A spectrogram of such an encounter appears in Figure 3d, with the sounds of each of the two individuals shown at the arrows.

TABLE 5

NUMERICAL DESCRIPTION OF THE POW CALL (N = sample size; $\overline{X}$ = mean; S.D. = standard deviation)

	N	$\overline{X}$	S.D.
Random sample			
Highest frequency in Hz	15	2407	383
Lowest frequency in Hz	15	953	264
Duration in seconds	15	0.062	0.015

Dance sequences accompanied by pows

	Females Present ?	N	Percent
25 April	no	20	10
26 April	yes	20	95
9 May	no	20	40
9 May	yes	20	80
16 May	no	20	40

Although the basic aggressive nature of the sounds seemed obvious, it appeared to me that differences in the sound from different individuals at different times might be related to the relative dominance or submissiveness of an individual in a given encounter. Unfortunately, I did not collect data with such analyses in mind and have no further information about this vocalization.

Cluck. Males frequently gave a soft cluck during periods of inactivity on the lek. Late in the morning, and particularly late in the season, when long periods of inactivity were common, individuals wandered about slowly, feeding on seeds and nipping at grass or leaves. The cluck was heard only during these times. It was not uncommon for birds to wander away from the lek, and clucks could be heard occasionally from the surrounding grass. Due to the softness, I was unable to obtain good recordings, and thus cannot demonstrate this vocalization spectrographically.

Female vocalizations. Female Sharp-tailed Grouse were normally quiet on the lek. Evans (1961) reported that they occasionally danced. I observed females give low intensity abbreviated gobbles on three occasions (see Figure 2e). It was similar to the male gobble except only two notes were present, with an upward stroke preceding the first. The first note had sound energy concentrated in two bands at 400 and 800 Hz. The second note had sound energy concentrated at 350 and 700 Hz. The overtones appeared to be harmonics. Total duration was 0.26 second.

Function is unknown though similarity to male vocalizations suggests a similar function (see below).

RESULTS

The dominant behavior on the lek changes from aggressive early in the season, to reproductive in mid-season, and finally to maintenance in nature late in the season. Based on the first season's study it seemed that the quantity of the various sounds made by males on the lek changed as the season progressed and that this change might be related to the predominant activity occurring at various times of the season.

During the early aggressive period males were actively engaged in establishing territories, overt aggression was common, and territorial boundaries fluid. Visits by strange males were common while females did not begin to visit until 15 April (Table 6). Note that six males were first present on 16 March but that visits were irregular until 11 April, when 13 males came. The weather from 16 March to 11 April was severe with temperatures well below freezing and snow frequent. Even on days when males were present, activity frequently was low. On 11 April, the number of males present was close to the maximum for the season and aggressive activity was high. It remained high for the next several days. It should be noted that fights were most common during the early season, particularly the first few days after males began coming regularly (Table 6). It was easy enough to recognize females by their behavior, but the recognition of strange males presented problems, particularly early in the season before resident birds were marked and while territorial boundaries were still fluid. I called any male which came to the lek after the others had arrived (resident birds almost always arrived together before sunrise), who was unable to successfully defend an area, and who was aggressively chased by resident birds until forced to leave, a strange male. Peripheral, but resident males, were frequently chased also, but always had an area on the periphery which was successfully defended. Strange males

TABLE 6

NUMBER OF BIRDS PRESENT ON THE EXPERIMENTAL LEK
AND THE NUMBER OF OBSERVED FIGHTS
(blank space indicates data
not available)

Date	Territorial Males	Strange Males	Females	Fights
16 March	6			
17	0			
18	0			
21	7			
1 April	0			
2	0			
6	8		0	
8	8	0	0	
9	8	0	0	
10	0	0	0	
11	13	8	0	45
12	11	5	0	19
14	13	1	0	12
15	16	0	1	
18	13	0	4	
23	15	1	4	7
24	15	1	9	2
25	15	0	2	
26	15	2	7	13
27	15	0	0	0
28	15	1	0	9
2 May	14	0	6	4
3	15	0	7	4
4	15	0	8	
6	13	0	2	6
8	14	1	2	13
9	13	0	2	0
11	13	0	0	0
16	11	0	0	0

TABLE 6--Continued

Date	Territorial Males	Strange Males	Females	Fights
18 May	11	0	0	0
19	11	0	1	6
20	11	0	1	0
21	11	0	0	0
23	11	0	0	0
28	11	0	1	9
30	10	0	0	0
1 June	11	0	0	0
2	11	0	0	0
9	11	1	1	4
11	9	0	0	0
15	9	0	0	0
18	9	0	0	0
23	9	0	0	0
1 July	0	0	0	0
5	0	0	0	0

visited most frequently early in the season, when overt aggression was most common (Table 6). Later in the season, fighting was frequent on days when females visited. This was to be expected since males moved toward the part of the lek where females were located, increasing the possibility of aggressive encounters with other males.

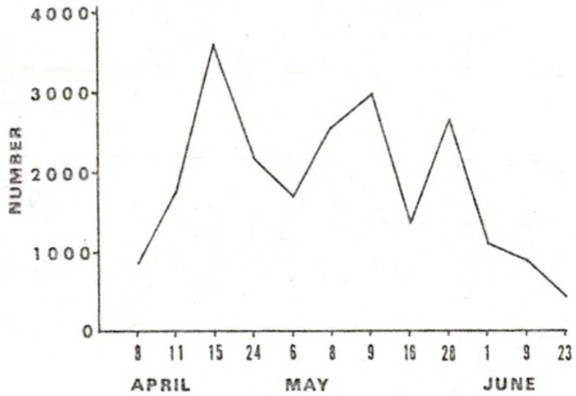
Once established, territories changed little (see maps, Figure 1). The only changes noted occurred when birds _1_ and _3_ failed to return after 4 May, and bird _4_ did not return after 16 May. Their territories were incorporated by neighboring males. Later in the season several peripherals failed to appear and their territories were likewise absorbed.

The total number of coos did not vary in a consistent seasonal pattern but rather appeared to fluctuate with changes in lek activities (Table 7; Figure 5a). Very early and very late in the season coos were relatively infrequent, as were other activities. Otherwise, coos seemed to occur early in the morning after resident males had arrived but prior to arrival of females, later in the morning after females had left, and any time when activity was low. Cooing birds were almost always in the center of their territories.

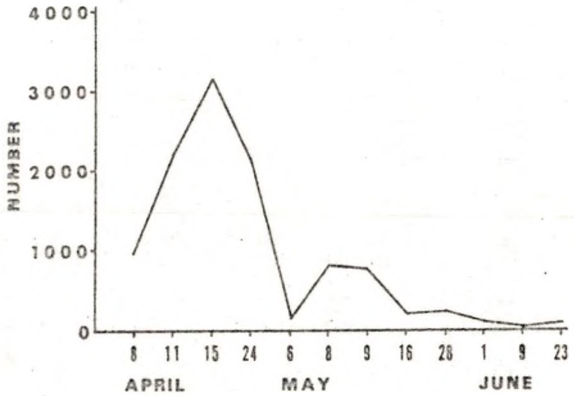
TABLE 7

TOTAL NUMBERS OF COOS, GOBBLES, DANCES, AND CHILKS COUNTED FROM TAPES

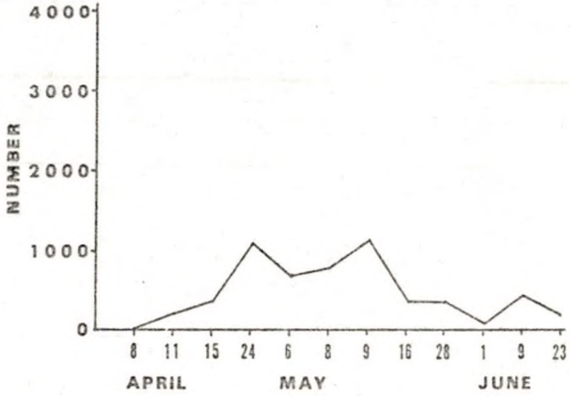
Date	Coos	Gobbles	Dances	Chilks	Notes
8 April	834	957	0	0	
11 April	1721	2190	209	97	
15 April	3638	3151	328	116	
24 April	2182	2095	1135	2489	
6 May	1726	167	624	2723	windy
7 May	1985	703	347	538	control lek
8 May	2510	784	753	2662	
9 May	2922	755	1177	3045	
16 May	1324	171	320	583	
28 May	2594	205	315	628	
1 June	1065	60	41	41	
6 June	26	0	0	1	control lek
9 June	913	16	397	552	
23 June	473	47	144	311	



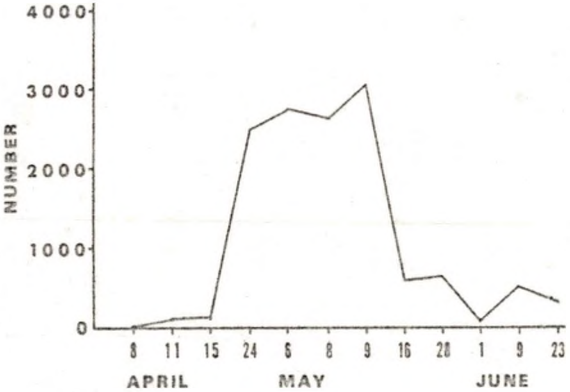
a. COOS



b. GOBBLES



c. DANCES



d. CHILKS

Gobbles were common early in the year but were rare by mid-season (Table 7; Figure 5b). Peaks of gobbling appeared to parallel peaks of fighting. Gobbling increased greatly when strange males appeared. One incident, especially, was of interest. Male 3 usually arrived separately and later than other resident males. On 11 April, while his territory remained vacant, a strange male appeared on the lek, was immediately chased by resident birds from territory to territory. This was accompanied by much gobbling from all residents. Finally, the stranger occupied the vacant territory. Birds in neighboring territories gathered around the periphery, engaged the stranger in numerous face-offs, and gobbled continuously. This continued for two minutes, when number 3 suddenly appeared, took possession of his territory and engaged the stranger in a fight lasting less than 10 seconds, whereupon the stranger flew to the top of my blind. The other males crowded around the blind, and gobbled continuously for nearly four minutes. He finally flew away; the others ceased vocalizing and resumed normal territory positions. Similar incidents were observed on 14 and 26 April.

The number of dances seemed to be related to the presence or absence of females (Table 7; Figure 5c). Note that no dances occurred until females began attending. Dances decreased when females ceased regular visits, except for a small peak 9 June when a single female appeared. Subjectively, dances always increased when females visited the lek. Although all or most males appeared to start and stop dancing in unison when females were present, this was not always the case. I feel that dancing occurred due to a stimulus provided by the female and that all males close to her received the stimulus simultaneously.

Numbers of chilks paralleled dancing frequency closely (Table 7; Figure 5d). In fact, chilks were commonly given during pauses between dance sequences, and, like dancing, increased greatly whenever a female appeared.

Data gathered on four individual birds during two half-hour periods at intervals through the season (described in Methods) showed the same pattern as above: gobbles were frequent early and declined rapidly; coos fluctuated greatly; dances and chilks were frequent during most of the mid-portion of the season. Additionally, these data suggested the maximum number of sounds an individual could produce in a given time period (Table 8).

TABLE 8

MAXIMUM NUMBER OF COOS, GOBBLES, DANCE SEQUENCES, AND CHILKS GIVEN BY ANY INDIVIDUAL BIRD IN ONE-HALF HOUR

Sound	Number	Bird	Date
Coos	125	4	8 May
Gobbles	199	4	24 April
Dance sequences	98	4	18 April
Chilks	126	4	8 May

There appeared to be a relationship between the presence of females and the number of _dances_ and _coos_. On days when females were present, more _dancing_ and less _cooing_ occurred during the half-hour period females were actually on the lek than when they were absent. In order to investigate this, _t_ tests were performed on the data with the null hypotheses that _dances_ and _coos_ occurred randomly and the presence of females had no effect (Table 9). Since values were highly significant, the null hypotheses were rejected and initial indications appeared to be confirmed.

TABLE 9

_t_ TEST ANALYSES OF NUMBER OF _DANCE_ SEQUENCES, _COOS_, _GOBBLES_, AND _FACE-OFFS_ IN RELATION TO FEMALE PRESENCE OR ABSENCE FOR FOUR MALES

Sound	No./Min. Females Present	No./Min. Females Absent	_t_ Value	Degrees of Freedom	Probability
Dance sequences	3.35	0.39	11.72	47	0.01
Coos	0.046	1.85	4.15	47	0.01
Gobbles	0.365	2.23	3.17	30	0.01
Face-offs	0.706	0.362	2.90	47	0.01

If _gobbling_ were related to aggressive behavior, one would expect it to be decreased when females were present and activity was reproductively oriented. A _t_ test was performed to test the hypothesis that female presence or absence had no effect on amount of _gobbling_ (Table 9).

Since gobbles were infrequent after 9 May, data after that date were not included. The value was highly significant and it was concluded that gobbles decreased when females visited.

Since gobbles decreased when females were present, what effect did female presence have on ritualized aggression--face-offs? A *t* test indicated face-offs increased when females visited (Table 9). This was not unexpected, since males moved toward females, thus increasing the chance of trespassing on another's territory resulting in a face-off.

PLAYBACK EXPERIMENTS

Results of playback experiments are summarized in Table 10. Coos and gobbles usually elicited coos by most of the birds present. The sound of dancing always elicited dancing by nearly every bird. Face-off chatter produced variable results, eliciting coos, gobbles, dances, face-offs, or flutter-jumps in no consistent order. Late in the season coos and face-off chatter elicited no responses.

The same tapes played on the control lek consisting of six males on 6 June, elicited responses essentially indistinguishable from late season responses on the experimental lek. I concluded that responses of males on the experimental lek were not strongly influenced by habituation to the recordings.

TABLE 10

REACTIONS OF MALES ON EXPERIMENTAL LEK TO PLAYBACKS OF FOUR SOUNDS COMPARED AS TO TIME OF SEASON AND TO THE CONTROL LEK

(figures in parentheses indicate number of episodes producing a given reaction)

Tape Segment	Time of Season	Predominant Initial Reactions	Other Reactions
Coos	Early	Coo in 30 sec. (5 of 5)	Face-off; gobble; flutter-jump
	Mid	Coo in 1 min. (3 of 5)	Dance (1 of 5); no reaction (1 of 5)
	Late	No reaction (5 of 5)	None
Gobbles	Early	Coo in 1-2 min. (5 of 5)	Dance; investigate sound source
	Mid	Coo in 2 min. (5 of 5)	Dance; gobble
	Late	Coo in 1 min. (2 of 5); none (3 of 5)	Dance; face-off
Dances and chilks	Early	Dance, chilk, flutter-jump in 30 sec. (5 of 5)	Face-off; gobble
	Mid	Same	Face-off
	Late	Same	Face-off
Face-off chatter	Early	Face-off in 1 min. (2 of 5); coo in 1 min. (2 of 5)	Dance; gobble; none (1 of 5)
	Mid	Highly variable	Highly variable
	Late	No reaction (5 of 5)	None
Coos	Control Lek Late Season	1 face-off in 15 sec. (2 of 3)	Dance; flutter-jump; no reaction
Gobbles		Coo in 15-30 sec. (3 of 3)	Investigate sound source; dance
Dances and chilks		Dance, chilk, flutter-jump in 30 sec. (3 of 3)	Face-off
Face-off chatter		No reaction	None

DISCUSSION AND CONCLUSIONS

The above descriptions include only those sounds made on the lek. It should be regarded as a tentative list for at least one sound has been described which I did not record (cackles by Lumsden, 1965).

Several methods of sound classification have been proposed. Thus Bremond (1963), on the basis of sound structure, divided bird sounds into songs, calls, and noises. Thorpe (1961), Stokes (1961), Marler (1956, 1960), and others have classified by function according to contexts in which sounds occurred and responses they elicited from conspecifics.

Adopting a functional classification, I have divided the seven sounds described above, into four categories: advertising (coo), reproductive (tail-rattling, chilk, and pow), aggressive (gobble and face-off chatter), and contact (cluck).

Several functional types of sounds are not given by Sharp-tails on the lek. Thus I did not observe distress, flight, parent-young contact, or alarm calls. Indeed, in 53 observed flying predator interactions, mostly Marsh Hawks (Circus cyaneus), the grouse invariably became alert and silent as the predator approached, then crouched in the grass, and flushed without vocal sound as the predator flew over the lek. Lumsden (1965) described a low "yur" call given by males on the lek as an alarm call, and suggested the sound of wings as the birds flushed might serve the same function. Sharp-tails flushed from the lek gave a "chuckle-chuckle" sound which may have been an alarm call.

Advertising Sounds

Höhn (1953) called attention to the similarity of the rookoing of the Black Grouse to the song of passeriforms. The booming of the Greater Prairie Chicken and the cooing of the Sharp-tailed Grouse are apparently homologous with rookoing (Hamerstrom and Hamerstrom, 1960). Borror (1961) states that the three main functions of passerine song are to advertize the presence of males, attract females, and repel other males. Thorpe (1961) adds the properties of individual and species recognition, locatability, and carrying power.

The coo of the Sharp-tail seems to fulfill most of these requirements. It is given season long, especially early in the morning just after males have arrived and before females are present. It differs from the boom of the Greater Prairie Chicken, the only closely related sympatric species, and is highly stereotyped allowing species recognition. Marler (1955, 1956) (Marler and Hamilton, 1966) discusses properties of sound governing the efficiency of locatability and carrying power. The coo is low in frequency which favors hearing over great distances and location by phase differences; commonly coos are repeated in long sequences and by many individuals in concert providing many sudden breaks and repetitions necessary for location by time differences.

Only the high frequencies best suited for location by intensity differences are absent. The aggressive function seems of less importance compared to the song of passeriforms, perhaps due to the nature of the social group. However, this vocalization is given only by territorial birds from within the territory, is associated with a visual display, and is released by an aggressive vocalization (gobble) as well as by cooing, suggesting it does function to warn conspecific males and to indicate territorial occupancy.

The work of Weeden and Falls (1959) demonstrating that Ovenbird (Seiuras aurocapillus) males can recognize individuals by sound alone and tell neighbors from strangers, suggests the same might occur in grouse, and if the coo is analogous to passerine song this vocalization would seem to be the most logical one for individual recognition. At this time I do not believe Sharp-tails use the coo for individual recognition due to the small male to male variation in frequency and duration.

Reproductive Sounds

It is difficult to separate reproductive and aggressive behavior. Frequently, courtship behavior appears to be the result of relative and absolute strengths of attack, escape, and sexual tendencies (Stokes, 1961). Tinbergen (1951, 1953) has pointed out how courtship behavior may be derived from aggressive behavior through ritualization to serve the purposes of attraction, appeasement, and synchronization. It is not surprising, then, to find both aggressive and sexual elements in the courtship displays and associated sounds of the Sharp-tailed Grouse. In this study dancing and associated tail-rattling did not become common until females began visiting the lek; and it increased with regard to sequence length and click rate when females were actually present. That some dancing occurred when only males were present, was associated with a visual display containing elements found in the face-off display, and occasionally was included in territorial boundary encounters suggests some aggressive function. It seems likely that dancing as a reproductive display represents ritualization of mainly aggressive behavioral elements. The tail-rattle could have evolved from the rapid tail flick seen in males engaged in a face-off (see Evans, 1961, for a description of the tail flick); the foot stomping from the rapid movements of the low advance; and the head down-wings out posture from the aggressive posture seen in the face-off.

Chilks appear to be so closely related to dancing that a similar function seems likely. The broad frequency range, abruptness, and tendency for repetition suits this vocalization for location by phase, intensity, and time differences. Variability in duration and frequency spectrum suggests the possibility of individual recognition.

The pow call occurred only during dance sequences and appeared closely related to the presence of females. Frequency varied considerably in the population, but since I have no data on individuals I cannot assess the possibility of individual recognition.

I believe the *tail-rattle*, *chilk*, and *pow* are mainly concerned with attracting and stimulating females after they have arrived on the lek. It does not seem likely that selection for individual recognition of males by females would have occurred since presumably a female normally visits the lek once for fertilization, and other factors seem to be involved in mate selection (see Lumsden, 1965, and Robel, 1966, 1967, for discussion of mate selection in grouse).

Aggressive Sounds

Evidence indicating an aggressive function for the *gobble* seems overwhelming. *Gobbles* were common only during the aggressive early part of the season, paralleled peaks of fighting, increased when strangers intruded, decreased when females were present, elicited *coos* (location and warning) on experimental playback, and provided the individual differences and stereotypy necessary for individual recognition. Marler (1960) points out that the need for species recognition tends to keep songs stereotyped, but individual recognition requires variability. That some birds are able to recognize and distinguish individuals was pointed out above (Weeden and Falls, 1959). In the case of a lek species like the Sharp-tail, the *coo* adequately provides for species recognition but may not provide adequate variation for individual recognition and may have lost part of its repelling function. The gobble appears to have the individual variability and locatability to provide the latter.

The aggressive nature of face-off chatter seems obvious enough to need no further discussion. However, my observations indicate there may be differences in the nature of the sounds given by the dominant and submissive bird in any encounter. It is my impression that the dominant bird holds his head higher and utters stacatto chatter at higher frequency, while the sounds of the submissive bird are lower pitched and more of a whine.

Contact Call

The low cluck, heard only during periods of inactivity, seems similar to the "all is well" call of the Chukar (*Alectoris graeca*) (Stokes, 1961). It may allow grouse to keep in contact with each other, particularly while feeding in heavy cover.

Robel (1966, 1967) stated that Greater Prairie Chicken leks functioned in attraction of females and selection of the fittest males to perform most of the copulations. Lumsden (1965), in addition, suggested the function of population regulation. Wynne-Edwards (1962), discussed population regulation in grouse, stating that the lek provided an external reference for dominance and controlled dispersion of the population, the basic functions of territory. Since there appeared to be an optimum lek population size for maximum reproductive success, and leks tended to be separated by a distance equal to the carrying power of the sounds produced by males (Wynne-Edwards, 1962)., in years when population numbers were high, surplus males were excluded from leks, and extreme competition for females resulted in interference with mating (i.e., "knocking off" a male attempting copulation). Thus large lek population in high population years produced relatively fewer offspring, resulting in population decline.

It is not possible to separate discussions of lek function from lek evolution. If we presume that lek inhabiting grouse species, which for the most part occupy open exposed habitats, evolved from one or more ancestral, solitary, forest species, then lek behavior should be interpreted from the point of view of adaptation to a new environment. Compared to the forest, the prairie is open and exposed. A grouse population living solitarily in such an environment would be easy prey for aerial predators. It appears to me that the lek may represent an adaptation to predator pressure resulting in communal association for mutual protection. The intricate and ritualized social system represents adaptation to the need for close association. The basic functions of territory as seen in monogamous species remains. Ritualization of behavior, especially aggressive, evolved to prevent injury and conserve energy. Vocalizations too are among those behaviors which underwent considerable modification. The coo assumed the basic species-specific attraction and location function. The gobble assumed an aggressive function largely restricted to a short period of overt aggression. Aggressive behavior and associated sounds (face-off) became ritualized and modified to assume reproductive function (dancing).

Obviously, much work remains to be done before lek function and evolution will be understood. Similar studies need to be done on other leks. Studies of stimulus-response interactions must be conducted with clearly defined problems and goals in mind. Kruijt and Hogan (1967) have pioneered this approach in their studies of Black Grouse. Experimental approaches, especially playback experiments on a number of leks with better control and emphasis on individual differences, responses, and identification, must be executed. Recent advances in motion picture equipment now allow entire morning time-lapse studies at reasonable expense. Physiological studies, such as that of Trobec (1970) implanting selected males with testosterone propionate, may help determine function and causation of behavior, and need to be done with better control and on several leks simultaneously. In addition, comparative studies of various forest and open country grouse need to be conducted in order to give indications as to how and why leks and attendant behavior evolved.

Behavior of females on the lek has been little studied. Perhaps this is because they only visit for short periods, are generally silent, and engage in no apparent displays. However, techniques for studying female behavior need to be developed and detailed studies of male-female interactions made before behavior on the lek will be completely understood.

SUMMARY

Acoustical behavior of Sharp-tailed Grouse on the lek was studied during the spring of 1970. During the early portion of the season activity was largely aggressive, territorial boundaries fluid, visits by strange males common, and female visits uncommon. Predominant acoustical signals were aggressive, stereotyped, and involved in species and individual location and recognition. During mid-season, females visited, were courted by males, and copulations occurred. Acoustical signals were concerned with attracting and stimulating females, varied on a time and frequency continuum, and thus were not as highly ritualized. During the last portion of the season, activity tapered off and acoustical signals diminished.

Seven distinct male sounds and one female sound were distinguished, and divided into advertising, reproductive, aggressive, and contact categories.

Coos were relatively stereotyped in frequency and duration, and provided cues for location over long distances. They were common season-long but diminished when females visited. Playback of coos elicited cooing. Probable functions include species recognition, territory advertisement, and individual location. Compared to passeriform song, *coos* did not show a strong aggressive function.

Tail-rattling (*dancing*) was most common during the mid-portion of the season when females were visiting regularly, particularly when females were actually present. Length of sequences and click rate increased when females were present. *Chilks* paralleled *dancing* closely, varied in frequency and duration, and provided good location cues. Playback of these two sounds together elicited *dancing* and *chilks*. The *pow call* occurred only in conjunction with *dancing* and was most common when females were present. These three sounds appeared to function in attraction and stimulation of females.

Gobbles were highly stereotyped, showed specific individual differences and gave good location cues. They were common during the early aggressive part of the season but declined rapidly by mid-season, increased greatly when strange males visited, but decreased when females were present. Playback of *gobbles* elicited *cooing*. The function of the *gobble* seemed to be largely aggressive.

Face-off chatter was associated with ritualized fighting at territorial boundaries and varied greatly in frequency and pattern. Playback of this sound elicited variable reactions. Differences in this sound shown by individuals in an encounter may be related to their relative dominance.

The cluck occurred only during periods of inactivity and appeared to be a contact call.

Females were usually silent but occasionally gave an abbreviated gobble, the function of which was unclear.

It was not possible to separate discussion of lek function and evolution. Presumably, open country lek grouse evolved from solitary forest species. Predator pressure of an exposed environment forced new adaptations including communal association for mutual protection. The need for close association, then, led to development of the intricate and ritualized social system.

The need for future studies was discussed including stimulus-response interactions, playback experiments, physiological studies, and comparative studies on other grouse species.

LITERATURE CITED

Borror, D. J. 1961. Intraspecific variation in passerine bird songs. Wilson Bull., 73: 57-78.

Bremond, J. C. 1963. Acoustic behavior of birds. In Acoustic Behavior of Animals, R. G. Busnel, Ed., 710-750. Elsevier Publish. Co., New York.

Evans, K. E. 1968. Characteristics and habitat requirements of the Greater Prairie Chicken and Sharp-tailed Grouse--a review of the literature. USDA Conserv. Res. Rep. No. 12.

Evans, R. M. 1961. Courtship and mating behavior of the Sharp-tailed Grouse (Pedioecetes phasianellus jamesi, Lincoln). Unpubl. M.S. Thesis, Univ. of Alberta, Edmonton.

Hamerstrom, F. and F. Hamerstrom. 1960. Comparability of some social displays of grouse. Proc. xii Int. Orn. Cong., Helsinki, 1958. 274-293.

Höhn, E. O. 1953. Display and mating behavior of the Black Grouse, Lyrurus tetrix. Anim. Behav., 1: 48-58.

Kruijt, J. P. and J. A. Hogan. 1967. Social behavior on the lek in the Black Grouse, Lyrurus tetrix. Ardea, 55: 203-238.

Lumsden, H. G. 1965. Displays of the Sharptail Grouse. Res. Rep. No. 66, Ontario Dept. of Lands and Forests, Maple.

Marler, P. 1955. Characteristics of some animal calls. Nature, 176: 6-8.

________. 1956. The voice of the Chaffinch and its function as a language. Ibis, 98: 231-261.

________. 1960. Bird songs and mate selection. In Animal Sounds and Communication, W. E. Lanyon and W. N. Tavolga, Eds., 348-367. Amer. Inst. Biol. Sci., Washington, D. C.

Marler, P. and W. J. Hamilton III. 1966. Mechanisms of Animal Behavior. John Wiley and Sons, Inc., New York.

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

_________. 1966. Booming territory size and mating success of the Greater Prairie Chicken (*Tympanucus cupido pinnatus*). Anim. Behav., 14: 328-331.

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

Stokes, A. W. 1961. Voice and social behavior of the Chukar Partridge. Condor, 63: 111-127.

Thorpe, W. H. 1961. Bird-song. Cambridge Univ. Press, Cambridge.

Tinbergen, N. 1951. The Study of Instinct. Oxford Univ. Press, London.

_________. 1953. Social Behavior in Animals. Methuen and Co., Ltd., London.

Trobec, R. J. 1970. Effects of testosterone propionate implantation on lek behavior of the Sharp-tailed Grouse. Unpubl. M.S. Thesis, Univ. of North Dakota, Grand Forks.

Weeden, J. S. and J. B. Falls. 1959. Differential responses of male Oven-birds to recorded songs of neighboring and more distant individuals. Auk, 76: 343-351.

Wynne-Edwards, V. C. 1962. Animal Dispersion in Relation to Social Behavior. Hafner, New York.