

QUANTITATIVE ANALYSIS OF PRAIRIE GROUSE VOCALIZATIONS

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ABSTRACT.—The structure of homologous vocalizations of Greater Prairie-Chickens (*Tympanuchus cupido*) and Sharp-tailed Grouse (*T. [Pedioecetes] phasianellus*) was studied during four mating seasons in northwestern Minnesota. In this region males of the two species form display grounds in similar areas and occasionally occur together in mixed grounds where they hold mutually exclusive territories. Hybrids constitute approximately 3% of the combined populations. This study tested the hypothesis that the structures of homologous vocalizations varied predictably with function to assist in reproductive isolation. Aggressive calls were more similar between the species than courtship calls. The dichotomous nature of the birds' vocal systems could promote heterospecific spacing and inhibit mating. The calls of two hybrid males varied in complex ways from those of either parental species.

Although prairies are poor environments for transmission of acoustical signals, both species of grouse depend heavily on vocalizations in their communication. Sound transmission is enhanced in these species by low frequencies, use of "sound windows," and crepuscular displaying.

Greater Prairie-Chickens (*Tympanuchus cupido*) and Sharp-tailed Grouse (*T. phasianellus*; A.O.U. 1982) are sympatric through a narrow zone in the midwestern and north central United States. In this zone hybridization typically occurs at a rate of 1–3% of the parental populations (Johnsgard and Wood 1968, Sparling 1980) although it has been recorded as high as 25% of the combined populations (Lumsden 1970). Ecological isolating mechanisms based on habitat preferences are weak, for males of both species frequently use the same areas for display grounds (Ammann 1957). Similarly, post-mating mechanisms are of little significance because hybrid females are fertile, their fecundity comparable to that in intraspecific matings (McEwen et al. 1969, Sparling 1980). Male hybrids however, may be unsuccessful in attracting mates. Several studies (e.g., Hamerstrom and Hamerstrom 1960, Lumsden 1965, Hjorth 1970, Johnsgard 1973) have suggested that displays may be very important in maintaining species integrity. Descriptions of visual displays, for example, indicate that courtship displays are very different between species while forms of agonistic behavior are similar. Through the use of playback experiments, I (Sparling 1981b) showed that vocalizations are also important for maintaining species integrity because both Greater Prairie-Chicken and Sharp-tailed Grouse males responded to some of the other species' aggressive calls.

The primary purpose of this paper is to further explain the role of vocalizations as isolating mechanisms between Greater Prairie-

Chickens (GPC) and Sharp-tailed Grouse (STG). I test the hypothesis that structural differences among homologous calls vary predictably with function. An underlying premise of this hypothesis is that homologous epigamic vocalizations are more different between species than agonistic vocalizations. This relationship between epigamic and agonistic vocalizations could result if this dichotomy decreased transfer of information between potential heterospecific mates while promoting spacing between aggressive individuals.

A second objective of this study is to examine relationships between the structure of calls and their functions. GPC and STG inhabit open grasslands where sound attenuation is especially high (Morton 1975, Marten and Marler 1977, Wiley and Richards 1978). Yet many of the vocalizations given by these birds, particularly the prairie-chicken "boom," are noted for their long traveling distances. This acoustical property is probably related to the structure of the signals and to the way in which they are emitted.

METHODS

STUDY SITE

The study area was a 210 km² mixture of small-grain farmland, pasture, homesteads and tall-grass prairie in northwestern Minnesota. STG were native in this area prior to white settlement but GPC probably became established in the late 1800's (Partch 1973).

From 1974–1978, other biologists and I found 15 display grounds in the area. Five of

these grounds were mixed (i.e., contained males of both species) in at least one year. The number of male GPC ranged from 70 in 1974 to 140 in 1978 while the number of male STG varied from 22 to 30. We also noted eight hybrid males, including two probable backcrosses and one or two F_1 hybrid females. Further details of population dynamics and habitat characteristics are in Sparling (1980).

OBSERVATIONS

I watched grouse daily from blinds located on the edges of display grounds from mid-February until early June of 1975–1978. In each season, two or three grounds were chosen for intensive study. These focal grounds were visited alternately so that observations could be divided among single and mixed-species display grounds. Each focal ground was visited one to three times per week.

I used 15 GPC, 18 STG and 15 hybrid forms of behavior to determine functional associations between vocalizations and other displays. During each day of observation these actions were recorded from randomly selected focal animals (Altmann 1974) during 5-min sessions taken every 20 min. A total of 12,363 GPC, 7,255 STG, and 1,694 hybrid acts were recorded. Data from all sessions were compiled into transition matrices whose rows and columns represented preceding and following acts, respectively. Correlations among columns were used to determine relationships among forms of behavior.

All birds used in this study were individually recognizable, because either they were color-banded or they held well-defined territories. Although I recorded and analyzed other vocalizations, I used only those from known territorial individuals. Calls from two F_1 hybrids were also analyzed. One hybrid held a central territory on the Pankratz GPC display ground for three years. The other held a peripheral territory on the West Tymp mixed display ground and was seen for one season.

TREATMENT OF VOCALIZATIONS

I recorded vocalizations with a Uher 4000 Report-L tape recorder at 19 cm/s using Uher 516 directional and Sennheiser 804 ultra-unidirectional microphones. Calls were analyzed with a Kay Elemetrics Co. Sonagraph 7029A at 20–2,000 or 40–4,000 Hz ranges, depending on call characteristics. Narrow-band sonograms were used to measure frequencies and wide band was used for temporal features. Terminology follows that of Shiovit (1975) except that the absolute difference between the lowest and highest trace of the strongest or carrier frequency is called “frequency range”

and a “sequence” consists of a train of notes or elements that are separated from other sequences by another type of call or by a long period of silence.

STATISTICAL ANALYSIS

Previous workers have suggested that song characteristics with little intraspecific variation may be potentially useful in species recognition. Thus Emlen (1972) and others have used coefficients of variation (CV) for single-species analyses. Other researchers (Goldstein 1978, Sparling and Williams 1978, Brown and Lemon 1979) have used multivariate techniques on vocalizations and found them better than univariate statistics in distinguishing populations or species. I employed both univariate and multivariate statistics in this study.

“Whoops” and “chilks,” “whines” and “cackles” were analyzed with discriminant analysis (Nie et al. 1975). This technique initially adds variables (call characteristics) to form a predictive model that maximally separates groups (species or hybrids). Significant variables (based on the change in Rao’s V , a measure of group dispersion) are then restructured into functions. Functions are extracted in descending order of the amount of accountable variance among groups (measured by eigenvalues) explained by a function. These functions are then used to classify existing data into groups and reliability of the model can be determined. Finally, group membership and call characteristics can be related through canonical correlation values. Further details of this procedure are given in Sparling and Williams (1978) and Aspey and Blankenship (1978).

Data used in these analyses were of two types. Sequence duration and number of notes were single observations per sequence. Note duration, internote interval and frequency characteristics were represented by mean values for each sequence. Standard deviations for repeated measures were initially included in analyses but were found to be unimportant in discriminating species. Intra-sequence variation, however, may be useful in distinguishing individual Sharp-tailed Grouse (unpubl. data).

RESULTS

FUNCTIONS OF VOCALIZATIONS

The functions and contexts of Greater Prairie-Chicken and Sharp-tailed Grouse vocalizations have been described (Hamerstrom and Hamerstrom 1960, Lumsden 1965, Hjorth 1970) and experimentally supported (Kermott and Oring 1975, Sparling 1981a). GPC “booms” occurred in a variety of contexts including mild aggressive interactions, early

TABLE 1. Correlations between vocalizations and other behaviors in prairie grouse.

Vocalization	Stand off	Fight	Stamping or dancing	Flutter jump	Comfort
<i>Greater Prairie-Chicken</i>					
Boom	-0.167	-0.186	0.503	-0.106	-0.149
Whoop	0.425	0.222	0.999*	0.965*	0.397
Whine	0.103	0.270	0.207	0.281	0.152
Cackle	0.740*	0.743*	0.054	0.107	0.300
<i>Sharp-tailed Grouse</i>					
Coo	-0.117	-0.052	0.066	-0.087	0.415
Chilk	-0.005	-0.103	0.929*	0.833*	-0.263
Whine	0.920*	0.995*	0.058	-0.255	0.160
Cackle	0.757*	0.880*	-0.011	-0.286	0.021
<i>Pankratz hybrid</i>					
Whoop	0.095	-0.072	0.987*	0.947*	0.127
Whine	0.777*	0.767*	-0.018	-0.036	0.703
Cackle	0.113	0.786*	0.113	0.145	0.008

* $P < 0.01$.

morning advertising, and when hens were present. Mild aggressive "booms" were softer, less resonant and frequently briefer than courtship-related "booms." As a result, only the latter type of "booms" were included in analyses. Because this call is given in a wide variety of situations, "booms" did not significantly correlate with any of the visual marker behaviors (Table 1), but they were significantly correlated with "whoops" ($r = 0.995$, $df = 17$, $P < 0.01$). "Booms" function primarily as long distance advertisers (they may be heard for more than 4 km) and as the principal courtship vocalization.

STG "coos" were structurally homologous to "booms" and also occurred in several contexts. "Coos" did not travel as well as "booms," possibly because they lacked resonance and were given less energetically than "booms." A

principal function of "coos" was as a tonic signal (Schleidt 1973) that denotes the presence of a male to both other males and females. As such it had both epigamic and aggressive connotations. Because "coos" occurred in many situations, they did not correlate with any visual marker.

GPC "whoops" and STG "chilks" were probably homologous although their relationship was less clear than with the other pairs of vocalizations. Both were clearly epigamic for they occurred significantly more often when hens were present and in early morning displaying than at other times. Moreover, "whoops" had high correlations with "stamping" and "flutter jump" while "chilks" correlated with "flutter jump" and "dancing," which are epigamic visual displays. The prin-

TABLE 2. Characteristics of "booms" and "coos."

Characteristic†		Greater Prairie-Chicken "booms"	Sharp-tailed Grouse "coos"	West Tymp hybrid "coos"	Univariate F-ratio‡
Number of notes per sequence	\bar{x}	2.73	21.71	1.50	
	SD	0.89	39.82	0.71	
	CV	32.6	183.4	47.3	29.070
Note duration	\bar{x}	2.73	0.22	0.33	
	SD	0.49	0.08	0.03	
	CV	17.9	36.4	9.1	7,548.670
Internote interval	\bar{x}	6.64	3.40	1.58	
	SD	3.88	4.07	2.24	
	CV	58.4	120.2	141.8	58.358
Strongest frequency	\bar{x}	268	297	342	
	SD	17	54	14	
	CV	8.0	18.2	4.1	11.642
Frequency range	\bar{x}	48	81	92	
	SD	18	4	14	
	CV	37.5	4.9	15.2	919.900
n^*		128	306	4	

† Temporal characteristics in seconds, frequency characteristics in hertz.

‡ F-ratios calculated between GPC and STG. Two-tailed values are all significant at $P < 0.005$, $df = 1, 432$.

* Sample sizes refer to number of sequences analyzed. Eleven GPC chickens, 11 STG and 1 hybrid were sampled.

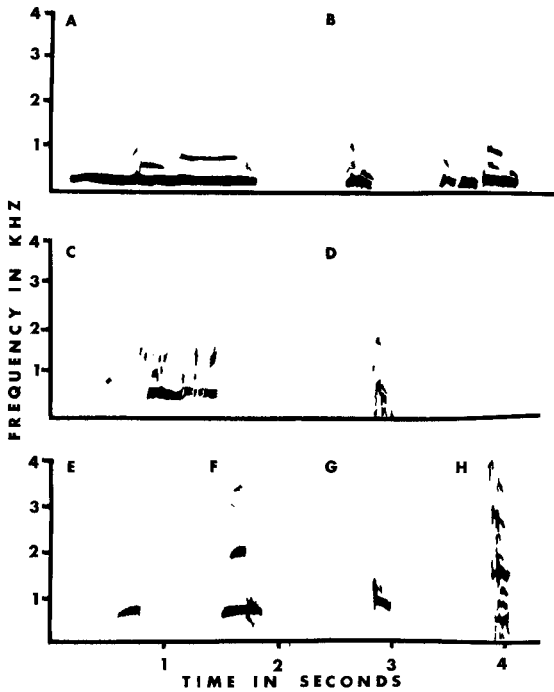


FIGURE 1. Tracing of some prairie grouse vocalizations. A—Greater Prairie-Chicken “booms”; B—Sharp-tailed Grouse “coos”; C—West Tympt hybrid “coom”; D—West Tympt hybrid “coo”; E—Greater Prairie-Chicken “whoop”; F—West Tympt hybrid “whoop” G—West Tympt hybrid “chilk”; H—Sharp-tailed Grouse “chilk.”

cial functions of these calls are to attract females at both medium and short ranges. Both vocalizations may also have been slightly agonistic among males because males of both species responded aggressively to playbacks of conspecific calls (Sparling 1981a).

The “whines” of both species were given in agonistic encounters such as “face-offs” or “stand-offs” when males opposed each other at territorial boundaries. STG “whines” were virtually restricted to this context but versions of GPC “whines” also occurred during “flutter jumps” and when a bird was alarmed, such as when seeing a possible predator. Only aggressive GPC “whines” were analyzed. “Whines” of both species had high correlations with agonistic “stand-offs” and “fights.”

“Cackles” of both GPC and STG occurred in similar contexts as “whines.” In agonistic encounters, however, “cackles” connoted a higher tendency of attacking and fighting than “whines.” “Cackles” were the most aggressive of the homologous calls analyzed in this study. In summary, the functional relationship of the calls compared here from most epigamic to most agonistic would be: booms, whoops and chilks, coos, whines, and cackles.

In addition to homologous vocalizations, two types of Sharp-tailed Grouse calls are exam-

TABLE 3. Characteristics of prairie grouse “whoops” and “chilks.”

Characteristics†		Greater Prairie-Chicken “whoop”	Sharp-tailed Grouse “chilk”	Pankratz hybrid “whoop”	West Tympt hybrid “whoop”	West Tympt hybrid “chilk”	Univariate F-ratio
Number of notes per sequence	\bar{x}	1.05	1.91	1.50	1.33	1.12	
	SD	0.22	1.09	0.92	0.65	0.35	
	CV	20.9	57.1	61.3	48.9	31.2	7.04**
Note duration	\bar{x}	0.27	0.09	0.48	0.43	0.23	
	SD	0.10	0.04	0.22	0.10	0.05	
	CV	37.0	44.4	45.8	23.2	21.7	56.82**
Internote interval	\bar{x}	0.01	0.07	0.06	0.15	0.13	
	SD	0.05	0.10	0.11	0.30	0.38	
	CV	500.0	152.8	183.3	200.0	292.3	2.43
Sequence duration	\bar{x}	0.30	0.28	0.70	0.71	0.38	
	SD	0.14	0.29	0.37	0.62	0.42	
	CV	46.7	103.6	52.9	87.3	110.5	6.96**
Lowest frequency	\bar{x}	465	889	462	729	380	
	SD	117	341	86	132	95	
	CV	25.2	38.3	18.6	18.1	25.0	22.45**
Strongest frequency	\bar{x}	623	1,401	678	767	926	
	SD	134	429	339	97	50	
	CV	21.5	30.6	50.0	12.6	5.4	40.38**
Highest frequency	\bar{x}	891	2,487	1,451	2,167	2,504	
	SD	436	1,021	395	1,055	1,268	
	CV	48.9	41.0	27.2	48.7	50.6	12.40**
Frequency range	\bar{x}	119	184	203	250	306	
	SD	75	158	73	115	149	
	CV	63.0	85.8	36.0	46.0	48.7	5.66*
$n\ddagger$		41	43	8	12	8	

* $P < 0.01$; ** $P < 0.002$. F-ratios are calculated over all groups, $df = 4, 107$.

† Temporal characteristics in seconds, frequency characteristics in hertz.

‡ Sample size refers to number of sequences analyzed. Nine GPC, 12 STG and two hybrids were sampled.

TABLE 4. Characteristics of prairie grouse "whines."

Characteristic†		Greater Prairie-Chicken	Sharp-tailed Grouse	Pankratz hybrid	West Tymp hybrid	Univariate F-ratio
Number of notes per sequence	\bar{x}	9.24	4.65	5.54	16.40	
	SD	9.10	2.98	1.86	9.14	
	CV	98.5	64.1	33.6	55.7	10.615**
Note duration	\bar{x}	0.19	0.37	0.16	0.27	
	SD	0.06	0.13	0.05	0.07	
	CV	31.6	35.1	31.2	25.9	29.392**
Internote interval	\bar{x}	0.20	0.34	0.28	0.23	
	SD	0.09	0.24	0.24	0.11	
	CV	45.0	70.6	85.7	47.8	4.274*
Total duration	\bar{x}	4.63	4.52	3.54	6.93	
	SD	6.16	12.58	5.01	3.54	
	CV	133.0	278.3	141.5	51.1	0.250
Number of freq. bands	\bar{x}	3.86	5.43	3.58	2.88	
	SD	0.88	9.59	0.86	0.50	
	CV	22.8	176.6	24.0	17.4	0.762
Lowest frequency	\bar{x}	429	367	365	455	
	SD	288	126	139	66	
	CV	67.1	34.3	38.1	14.5	1.092
Strongest frequency	\bar{x}	989	867	836	831	
	SD	542	1,208	502	131	
	CV	54.8	139.3	60.0	15.8	0.201
Highest frequency	\bar{x}	2,033	1,211	1,938	1,333	
	SD	405	295	470	301	
	CV	19.9	24.4	24.2	22.6	44.670**
Frequency range	\bar{x}	281	238	232	106	
	SD	155	273	109	62	
	CV	55.2	114.7	47.0	58.5	1.933
$n\ddagger$		42	49	11	10	

* $P < 0.01$; ** $P < 0.002$. F-ratios are calculated over all groups, $df = 3, 118$.

† Temporal characteristics in seconds, frequency characteristics in hertz.

‡ Sample size refers to number of sequences analyzed. Nine GPC, 14 STG and two hybrids were sampled.

ined briefly to complete the species' repertoire. "Gobbles" were highly aggressive vocalizations given most often by males from the periphery of their territories during early spring when territories were being established. "Cork notes" were epigamic calls that occurred in similar contexts as "chilks."

GENERAL CHARACTERISTICS OF VOCALIZATIONS

GPC "booms" and STG "coos" (Fig. 1A, B) differed significantly in all the characteristics measured (Table 2), most conspicuously in note duration. Strongest and highest frequencies were the least variable characteristics in both species but their potential value as species identifiers was low due to extensive overlap between species. Number of notes per sequence and interval between notes appeared to be too variable to be useful in species recognition but may help distinguish individuals. "Booms" but not "coos" were frequently separable into 2–4 segments lasting 0.3–1.0 s that were distinguished by sharp breaks in frequency or amplitude. These segments and other differences made further analysis of "booms" and "coos" unnecessary.

"Coos" of the West Tymp hybrid (Fig. 1D)

could be distinguished from STG "coos" by number of notes, note duration and frequency characteristics. The Pankratz hybrid did not utter "coos" but all hybrids including these two had "cooms," which were intermediate between "booms" and "coos" (Fig. 1C). Unfortunately, "cooms" were very soft and infrequent and could not be quantitatively analyzed.

GPC "whoops" (Fig. 1E) and STG "chilks" (Fig. 1H) overlapped in number of notes, note duration, internote interval, sequence duration and frequency range (Table 3). Lowest and strongest frequencies did not overlap appreciably between species and low CV's indicated that they could be used for species recognition. The calls of the hybrids were intermediate in number of notes and frequency characteristics, but the West Tymp hybrid's calls (Figs. 1F, G) clearly differed from those of parental species in note duration, internote interval and frequency range. The calls of the two hybrids could best be discriminated from each other by frequency characteristics.

Temporal characteristics were more different than frequency characteristics in "whines" of these two prairie grouse (Fig. 2A–C, Table 4). Coefficients of variation for the parental

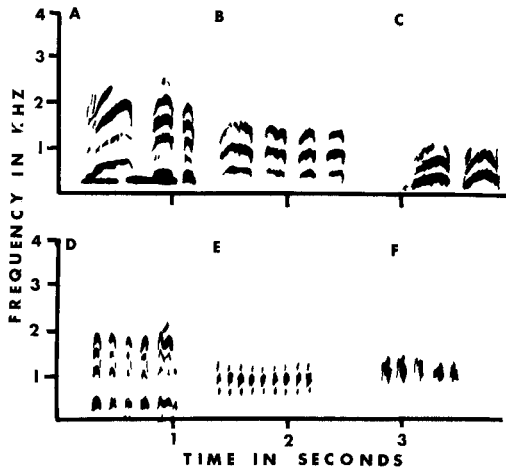


FIGURE 2. Tracings of prairie grouse "whines" and "cackles." A—Greater Prairie-Chicken "whines"; B—Pankratz hybrid "whines"; C—Sharp-tailed Grouse "whines"; D—Greater Prairie-Chicken "cackles"; E—Pankratz hybrid "cackles"; F—Sharp-tailed Grouse "cackles."

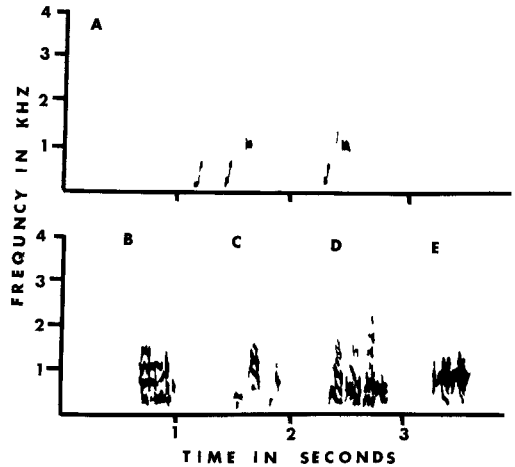


FIGURE 3. Tracings of "cork notes" and "gobbles" from Sharp-tailed Grouse and hybrids. A—three "cork notes" from a Sharp-tailed Grouse; B—C—two "gobbles" from different Sharp-tailed Grouse; D—"gobble" from Pankratz hybrid male; E—"gobble" from West Tympt hybrid.

species indicated that note duration and highest frequency were potentially useful in species recognition. However, low CV's for one species were often matched by high CV's in the other.

Hybrid "whines" could not be separated consistently from those of either parental species.

"Cackles" differed significantly between species only in number of notes and sequence duration (Fig. 2D–F, Table 5). The two grouse

TABLE 5. Characteristics of prairie grouse "cackles."

Characteristic†		Greater Prairie-Chicken	Sharp-tailed Grouse	Pankratz hybrid	West Tympt hybrid	Univariate F-ratio
Number of notes	\bar{x}	9.92	25.72	7.67	46.25	
	SD	7.25	26.53	4.73	2.68	
	CV	73.1	103.1	61.7	5.7	13.628*
Note duration	\bar{x}	0.05	0.08	0.04	0.09	
	SD	0.01	0.12	0.01	0.005	
	CV	20.0	150.0	25.0	5.50	2.604
Internote interval	\bar{x}	0.08	0.10	0.05	0.12	
	SD	0.02	0.15	0.01	0.01	
	CV	25.0	150.0	20.0	8.3	0.640
Sequence duration	\bar{x}	1.25	4.30	0.70	8.88	
	SD	1.01	7.70	0.36	0.62	
	CV	80.8	179.1	51.4	7.0	7.528*
Number of freq. bands	\bar{x}	4.59	4.39	3.72	3.95	
	SD	1.39	5.59	0.62	0.09	
	CV	30.3	127.3	16.7	2.3	0.134
Lowest frequency	\bar{x}	379	574	404	337	
	SD	239	964	222	11	
	CV	63.1	167.9	54.9	3.3	0.949
Strongest frequency	\bar{x}	760	746	1,012	811	
	SD	480	242	306	121	
	CV	63.1	32.4	30.2	14.9	0.388
Highest frequency	\bar{x}	1,665	1,365	1,354	1,217	
	SD	455	859	310	66	
	CV	27.3	62.9	22.9	5.4	2.423
Frequency range	\bar{x}	100	196	93	53	
	SD	75	375	20	33	
	CV	75.0	191.4	21.5	62.3	1.727
$n\ddagger$		72	29	4	4	

* $P < 0.002$. F-ratios calculated for parental species only, $df = 1, 99$.

† Temporal characteristics in seconds, frequency characteristics in hertz.

‡ Sample size refers to number of sequences analyzed. Ten GPC, nine STG and two hybrids were sampled.

TABLE 6. Characteristics of Sharp-tailed Grouse and hybrid "gobbles."

Characteristic		Sharp-tailed Grouse "gobbles"	Pankratz hybrid "gobbles"
Number of notes	\bar{x}	3.83	4.33
	SD	1.16	0.51
Duration of notes			
Note 1	\bar{x}	0.06	0.12
	SD	0.03	0.02
Note 2	\bar{x}	0.06	0.12
	SD	0.02	0.03
Note 3	\bar{x}	0.04	0.08
	SD	0.02	0.02
Note 4	\bar{x}	0.02	0.11
	SD	0.03	0.03
Internote intervals			
Interval 1	\bar{x}	0.03	0.03
	SD	0.02	0.02
Interval 2	\bar{x}	0.03	0.02
	SD	0.02	0.01
Interval 3	\bar{x}	0.02	0.02
	SD	0.02	0.02
Total duration	\bar{x}	0.29	0.54
	SD	0.10	0.06
Frequency characteristics of first note			
Number of freq. bands	\bar{x}	4.12	3.00
	SD	1.19	0.89
Lowest frequency	\bar{x}	252	288
	SD	136	23
Strongest frequency	\bar{x}	1,213	554
	SD	1,721	66
Highest frequency	\bar{x}	1,240	1,287
	SD	989	466
Frequency range	\bar{x}	302	223
	SD	91	823
n^a		142	6

^a Sample size refers to number of gobbles analyzed. A total of eight STG and one hybrid were used in the analysis.

overlapped in all of the characteristics, due largely to the high amount of STG variation. Both hybrids were represented by only four sequences each but the calls of the West Tymp hybrid differed from those of parental species in number of notes, sequence and note duration. The Pankratz hybrid had fewer notes and higher strongest frequencies than either parental species.

In general, univariate statistics showed several differences between calls of Greater Prairie-Chickens and Sharp-tailed Grouse. Temporal characteristics appeared to be more distinctive than frequency characteristics in "boom"/"coo" and "whoop"/"chilk" comparisons but the reverse was true for "whines" and "cackles." Comparable calls of hybrids appeared to be recognizable from each other and from parental calls but general relationships among the calls of GPC, STG, and hybrids

were difficult to discern. Coefficients of variation and intraspecific overlap were complementary for relatively few variables and were contradictory for several others.

OTHER VOCALIZATIONS

In addition to the homologous vocalizations described above, STG gave "gobbles" and "cork notes" (Fig. 3). "Cork notes" were limited to epigamic contexts and were soft, frequently repeated calls composed of one to three different sounds. The two most frequently occurring components were a low frequency, highly modulated introductory note which sounded like a cork popping from a bottle and a higher, pure tone reminiscent of a pebble plinking into water. A third, very brief element occasionally occurred between these two and was probably produced by rapid, lateral flicking of the rectrices. The two types of vocalizations can occur separately (see the first element of Fig. 3A), but I do not know if the tail-popping sound is independent.

"Gobbles" were threats that consisted of three to five notes, each separated by very short intervals and composed of intricate frequency structures (Table 6). These calls characterized individuals, in that preliminary discriminant analysis classified 10 individuals with over 80% reliability, based primarily on number of notes. All observed hybrid males gobbled. The "gobbles" of the Pankratz hybrid (Fig. 3C) differed from those of STG in note duration, total duration and strongest frequency of first note. The West Tymp hybrid's "gobbles" could also be clearly distinguished from those of STG (Fig. 3D).

DISCRIMINANT ANALYSIS OF HOMOLOGOUS VOCALIZATIONS

Stepwise procedures in discriminant analysis (Table 7) are useful in selecting variables that are most important in distinguishing species. In this analysis all eight variables used in stepwise analysis of "whoops" and "chilks" were significantly different. Note duration and strongest frequency accounted for 72% of group separation, while note duration and all frequency characteristics together accounted for 90% of the possible separation. In comparison to the other calls, the value of Rao's V was much higher, indicating a better distinction between "whoops" and "chilks." Only three characteristics were significant in stepwise analysis of "whines," and these resulted in the smallest Rao's V value. Stepwise analysis of "cackles" revealed nine significant variables, all with little ability to discriminate groups. The first eight of these variables accounted for slightly less than 90% of the total possible dispersion.

TABLE 7. Summary of stepwise discriminant analysis of some prairie grouse vocalizations.

Step	Variable entered	Rao's	F	df	Significance
"Whoops and chilks"					
1	Note duration	227.2	56.82	4,107	0.001
2	Strongest frequency	380.6	20.41	4,107	0.001
3	Highest frequency	416.7	7.07	4,107	0.001
4	Lowest frequency	458.3	7.63	4,107	0.001
5	Frequency range	476.1	3.27	4,107	0.001
6	Internote interval	491.8	2.18	4,107	0.004
7	Number of notes	512.9	2.70	4,107	0.001
8	Sequence duration	528.9	1.12	4,107	0.003
"Whines"					
1	Highest frequency	134.0	44.67	3,108	0.001
2	Note duration	209.8	12.35	3,108	0.001
3	Number of notes	235.9	8.25	3,108	0.001
4	Internote interval	243.4	1.36	3,108	0.058
"Cackles"					
1	Number of notes	40.9	13.63	3,106	0.001
2	Note duration	48.7	1.95	3,106	0.049
3	Total duration	91.0	13.20	3,106	0.001
4	Internote interval	127.2	9.62	3,106	0.001
5	Frequency range	150.6	4.91	3,106	0.001
6	Number of freq. bands	182.4	5.78	3,106	0.001
7	Lowest frequency	197.2	2.42	3,106	0.002
8	Strongest frequency	232.2	5.06	3,106	0.001
9	Highest frequency	261.3	5.83	3,106	0.001

Four significant functions could be extracted for "whoops" and "chilks" but the first two accounted for 91% of the variance among groups (Table 8). Only two significant functions were extracted each for "whines" and "cackles" and in both cases the significant functions accounted for more than 96% of the variance.

The first function extracted for "whoops" and "chilks" was comprised primarily of note duration and strongest frequency although both of these variables and highest frequency had their highest coefficients on the second function (Table 9). Thus function 1 of "whoops" and "chilks" represented a constellation of several characteristics while function 2 was primarily related to frequency. Similarly, function 1 for "whines" was composed primarily

of note duration and highest frequency while the second function was almost exclusively composed of number of notes. For "cackles," interval between notes, number of frequency bands, and lowest and highest frequencies loaded highest on the first function. Note duration, sequence duration and frequency range had their highest loadings on function 2.

GPC "whoops" and STG "chilks" were separated by both functions 1 and 2 (Fig. 4). They were most clearly distinguished from "chilks" and "whoops" of the West Tymp hybrid along the first function. Whoops of the Pankratz hybrid, however, substantially overlapped those of GPC. Confidence ellipses of West Tymp and Pankratz hybrid "whoops" demonstrated that they were the same type of call and that both differed from West Tymp hybrid "chilks."

TABLE 8. Extracted functions and statistics for prairie grouse calls.

Calls compared	Function	Eigenvalue	Percent of explained variance	Canonical correlation	χ^2 value	df	P
Whoop and chick	1	3.625	73.32	0.885	266.79	32	0.001
	2	0.876	17.72	0.683	106.76	21	0.001
	3	0.326	6.60	0.496	41.00	12	0.001
	4	0.116	2.35	0.323	11.49	5	0.042
Whines	1	1.958	86.89	0.814	144.70	12	0.001
	2	0.249	11.06	0.447	28.65	6	0.001
	3	0.046	2.05	0.210	4.84	2	0.089
Cackles	1	1.547	61.56	0.779	165.75	27	0.001
	2	0.878	34.96	0.684	71.79	16	0.001
	3	0.087	3.48	0.284	8.43	7	0.296

TABLE 9. Standardized discriminant function coefficients of prairie grouse call characteristics.

Characteristic	Function			
	1	2	3	4
	"Whoops and chilks"			
Number of notes	0.106	-0.220	0.112	1.018
Note duration	-0.610	-0.820	0.296	0.489
Internote interval	-0.086	-0.217	-0.332	-0.697
Lowest frequency	0.052	-0.332	1.008	-0.919
Strongest frequency	0.448	-0.512	-0.451	0.731
Frequency range	-0.033	-0.312	-0.686	-0.170
	"Whines"			
Number of notes	0.042	0.997	0.021	
Note duration	-0.406	0.198	1.196	
Internote interval	-0.101	-0.139	-0.722	
Highest frequency	0.685	-0.166	0.779	
	"Cackles"			
Number of notes	1.719	-2.541	2.208	
Note duration	-0.154	-3.162	0.850	
Internote interval	1.480	-0.137	4.152	
Sequence duration	-4.379	5.004	-3.757	
Number of freq. bands	0.800	-0.519	-1.295	
Lowest frequency	0.947	-0.500	-0.894	
Strongest frequency	-0.400	0.046	-0.330	
Highest frequency	0.119	0.680	0.801	
Frequency range	0.556	-0.577	-0.232	

Overall success of classification was 84.4%. Only one STG "chilk" was misclassified as a GPC "whoop." Twenty-nine percent of the hybrids' calls were misclassified with the majority of 'errors' resulting from calls being placed with GPC "whoops" or West Tymp hybrid "whoops" being misclassified as those of the Pankratz hybrid.

"Whines" were best recognized as to species along function 1 (Fig. 5). Hybrid and parental species "whines" were discriminated along the second function. Substantial overlap between GPC and Pankratz hybrid "whines" indicated that the calls were very similar.

Classification of "whines" was only 74.5% successful. Five percent (2) of the GPC calls were classified as STG while 2% (1) of the STG calls were placed with those of GPC. Twenty-one percent of the parental species' "whines" were placed in hybrid groups with the majority of errors occurring as GPC "whines" classified with those of the Pankratz hybrid.

"Cackles" were best recognized as to species along the second function but the two groups overlapped considerably (Fig. 6). Confidence ellipses also were placed closer together than for other calls. Thus "cackles" of both grouse were very similar. Sample sizes for hybrids were too small to calculate confidence ellipses but "cackles" of the Pankratz hybrid were obviously similar to those of GPCs while the West Tymp hybrid formed a distinct group.

Actual and classified groups of "cackles" agreed 76.5%. Ten percent of each parental

species calls were classified as belonging to the other species and 15% were placed in hybrid groups. Most misclassifications placed GPC "cackles" into the Pankratz hybrid's group. Hybrid "cackles" were all classified correctly, partly owing to small sample sizes.

DISCUSSION

Univariate and multivariate analyses both supported the hypothesis that homologous epigamic calls are more different between species than agonistic vocalizations. Analysis of variance showed that more characteristics were significantly different in "boom"/"coo" and "whoop"/"chilk" comparisons than between the two species' "whines" and "cackles." "Booms" and "coos" were the most species-distinctive of the four pairs of homologous calls—due to a segmented structure, long note duration and infrequent repetition of "booms." Because "booms" are both long-range advertisers and short-range courtship calls and "coos" are at least medium-range advertisers (Sparling 1981a), extreme divergence should be favored in this pair of calls. Similarly, differences in epigamic "whoops" and "chilks" would be advantageous if they were used in species identification.

Assuming that Greater Prairie-Chickens and Sharp-tailed Grouse had a common ancestor, as suggested by Short (1967), and that inter-specific mating results in lower reproductive success than intraspecific mating (Sparling 1980), divergence in epigamic calls could have

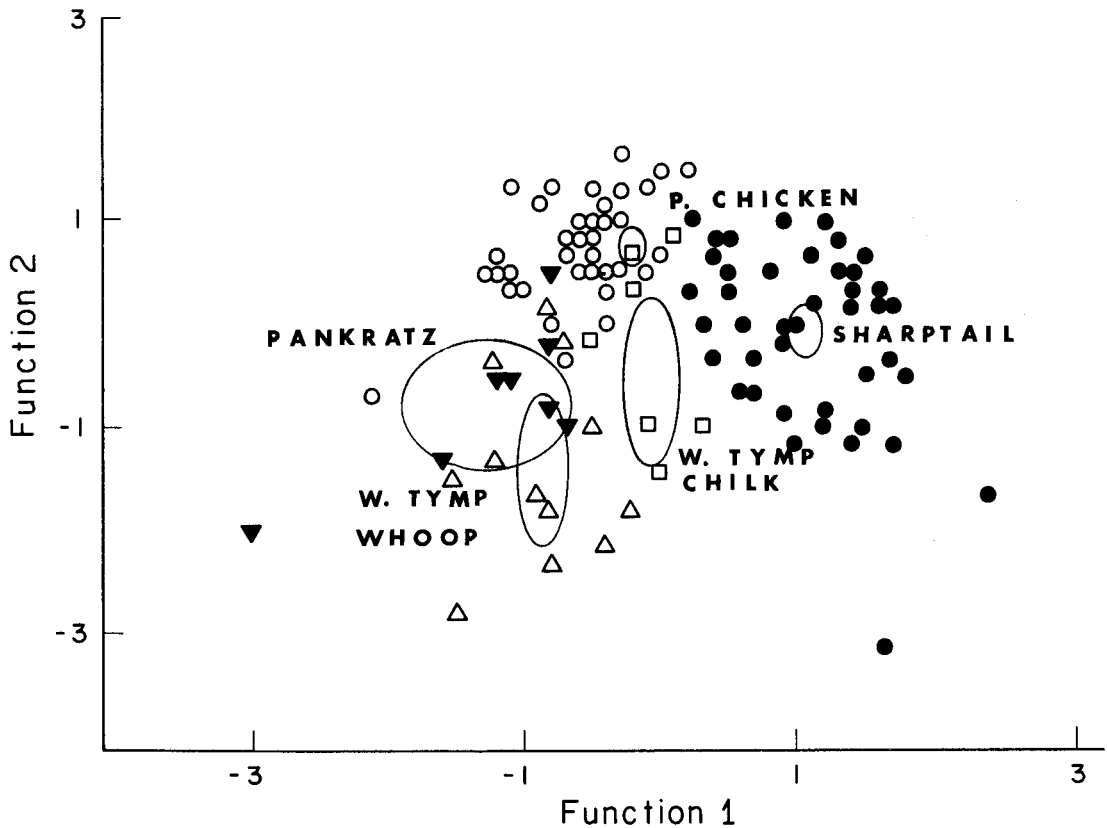


FIGURE 4. Discriminant analysis of prairie grouse "whoops" and "chilks." Empty triangles = West Tymp hybrid "whoops"; filled triangles = Pankratz hybrid "whoops"; empty squares = West Tymp hybrid "chilks"; empty circles = Greater Prairie-Chicken "whoops"; filled circles = Sharp-tailed Grouse "chilks."

been selected in two ways. Initial divergence may have resulted when ancestral populations settled different habitats, owing to properties of signal transmission in these areas (Morton 1975). Natural selection would then have favored improved discrimination by females if this either reduced energy and time spent in finding males of the same kind or reduced wasted reproductive effort from mating with a male of a different kind. Further divergence of vocalizations could have resulted if males with more distinctive calls attracted more mates.

Similarities in agonistic calls help promote spacing among the two species. Males of both species hold mutually exclusive territories on mixed display grounds and Sharp-tailed Grouse responded appropriately to playbacks of Greater Prairie-Chicken "cackles" (Sparling 1980, 1981b). While male GPC did not respond to playbacks of either their own or STG "cackles," they reacted aggressively to playbacks of STG "gobbles," and "cork notes." A conservative explanation for similarities in homologous aggressive calls of *Tympanuchus* grouse is that the vocalizations are not very different from those of a common ancestor.

Relationships among the two hybrids and the parental species were particularly interesting. The West Tymp hybrid was on a mixed lek and had a large vocal repertoire that included "booms," "coos," "whoops," "chilks," "gobbles" and "cork notes." He also gave appropriate species-specific calls when interacting with GPC or STG (Sparling 1979). His calls were either intermediate in structure between those of both species ("chilk," "whine") or very different ("cackles"). The Pankratz hybrid occupied a GPC ground and the only STG calls in its repertoire were "gobbles." Its "whoops," "whines" and "cackles" were very similar to those of GPCs. Unfortunately, the parentage of these hybrids is unknown and the relative importance of inheritance and learning in shaping the structure of these vocalizations remains undetermined. The intermediate characteristics of "booms" are probably due to genetic blending, however, as all hybrids in this study and others recorded in Ontario by H. G. Lumsden (tape available from the Cornell Laboratory of Ornithology) were very similar.

Prairie grouse are similar to other species studied in that several characteristics of vocal-

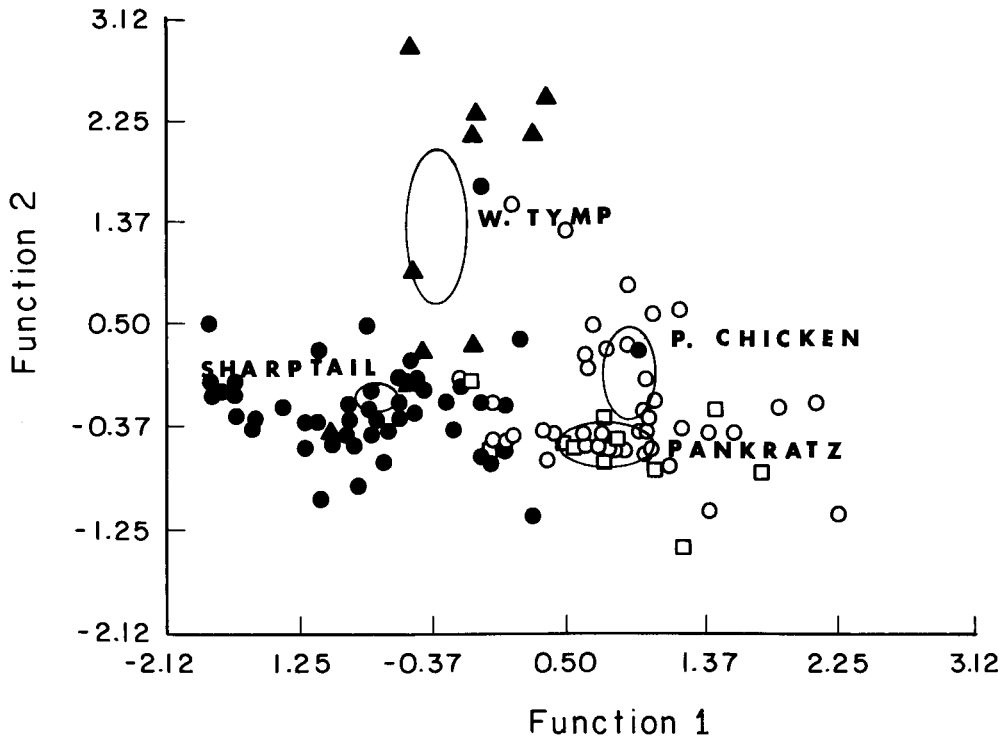


FIGURE 5. Discriminant analysis of prairie grouse "whines." Empty circles = Greater Prairie-Chickens; filled circles = Sharp-tailed Grouse; filled triangles = West Tympan hybrid; empty squares = Pankratz hybrid.

izations are useful in distinguishing species and probably in species recognition (e.g., Falls 1963, Emlen 1972). Each pair of homologous calls was separated along functions composed of several characteristics. Frequency characteristics tended to have smaller coefficients of variation and were more important in separating homologous "whines" and "whoops" from "chilks" than temporal features. Thus, frequency characteristics may be more important overall in species recognition. This premise is supported in that STG responded to GPC "cackles" and to "coos" that were temporally modified (Sparling 1979).

COMPARISON OF MULTIVARIATE AND UNIVARIATE METHODS

In general, the interpretations developed from univariate statistics were more muddled by overlap between species than those derived from multivariate analyses. Moreover, univariate statistics poorly represented relationships between hybrids and parental species. For "whoop"/"chilk," "whine," and "cackle" comparisons, discriminant analyses more adequately portrayed between species and species-hybrid associations. Although confidence ellipses did not overlap for any of the parental species' calls, they were closer for agonistic than for epigamic calls. Scattergrams (Figs. 4-6) showed that the epigamic "whoops" and

"chilks" were far more different between species than the polyvalent "whines," furthermore, "whines" were more different than the highly agonistic "cackles." When the structures of vocalizations from two or more groups or species are roughly similar, therefore, multivariate analysis may be better than univariate methods in showing similarities and differences. When two calls such as "booms" and "coos" are very different, elaborate analysis is not warranted.

ENVIRONMENTAL CONSTRAINTS

Morton (1975) and Marten and Marler (1977) showed that grasslands are poor environments for sound transmission. Excess attenuation is high in these areas because of thermal turbulence, high winds and ground absorption. Morton (1975) suggested that, in order to counteract this attenuation, grassland birds should either display in the air or have vocalizations with low carrier frequencies. For sound emitted at ground level in forest and edge habitats, he found a "sound window" of reduced excess attenuation between 1 and 3 kHz. Although he was unable to find a similar window in tropical grasslands, Marten and Marler (1977) identified one at similar frequencies in temperate grasslands.

Probably because flying requires much energy in birds with high wing loading, prairie

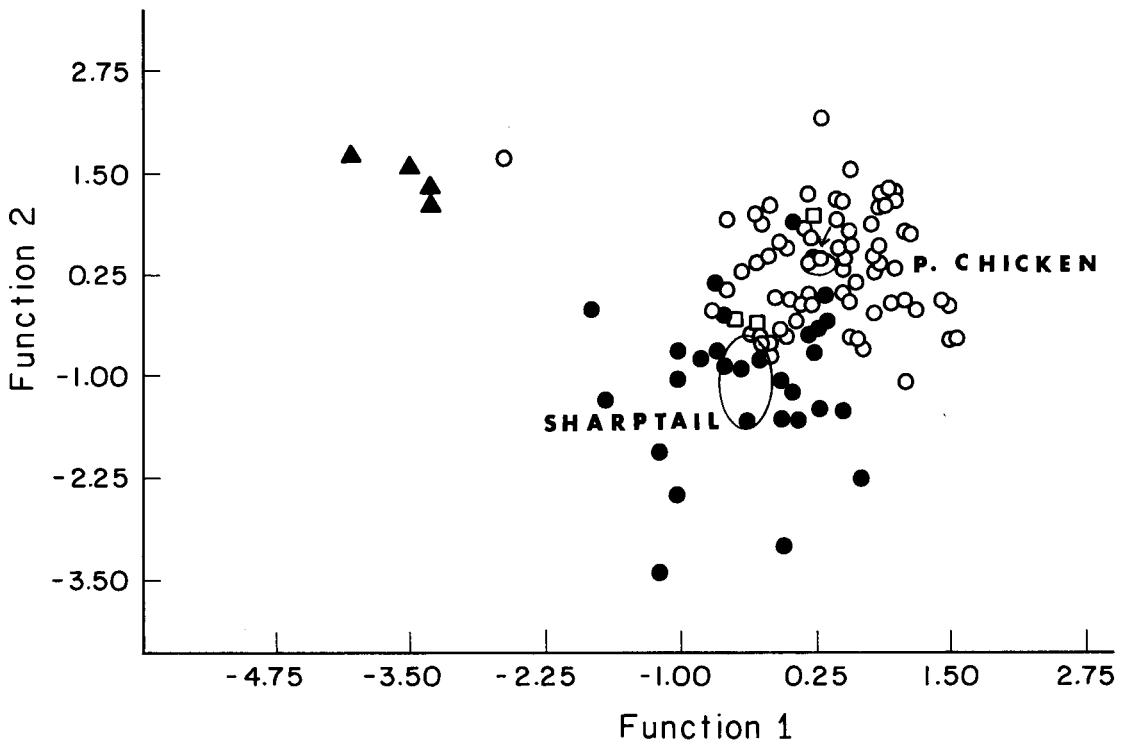


FIGURE 6. Discriminant analysis of prairie grouse "cackles." Empty circles = Greater Prairie-Chickens; filled circles = Sharp-tailed Grouse; filled triangles = West Tymph hybrid; empty squares = Pankratz hybrid.

grouse have only one aerial display—the "flutter jump." Although this display is often accompanied by modified "whines" and "cackles" in GPC, it probably has not evolved in order to increase the carrying power of these calls. Rather, the vocalizations appear to combine with jumping to help advertise a male's location. Support for these statements includes: 1) STG do not vocalize while "flutter jumping"; 2) "whines" and "cackles" also occur while a male sits or stands; and 3) even when he sits, a male's vocalizations are audible far off.

"Booms" and "coos" have very low carrier frequencies and are relatively pure tones. Both of these features would help in transmission but "booms" carry much farther than "coos." Part of this difference may be due to increased amplitudes and to larger resonating esophageal sacs ("air sacs") in GPC. STG "chilks" have carrier frequencies within the "sound window" range for open habitats but "whoops," "whines" and "cackles" have frequencies in a range of comparatively high excess attenuation (Marten and Marler 1977). Perhaps, as Wiley and Richards (1978) suggested for African primates, amplitude degradation in prairie grouse vocalizations can be used to determine a signaler's distance.

Daily patterns of activity may also help signal transmission. Male prairie grouse arrive on

display grounds about an hour before dawn and are most active until shortly after sunrise. They may also gather and display in the evening. Crepuscular activity may help signal transmission because wind and thermal turbulence are decreased at twilight. Although predation has sometimes been suggested as a factor responsible for crepuscular activity in grouse (e.g., Hjorth 1969, Hartzler 1974), diurnal predators take only a small proportion of displaying prairie grouse (Berger et al. 1963, Sparling and Svedarsky 1978). Nocturnal and crepuscular predators such as Great Horned Owls (*Bubo virginianus*) and Snowy Owls (*Nyctea scandiaca*) reduce defensive advantages of displaying in the early morning. Moreover, leks are usually in open areas where the many observers can spot a predator before it poses a serious threat. Thus, early morning displaying of prairie grouse may be related to signal transmission as much as predator defense.

I conducted my study in an area of sympatry where specific distinctiveness might be expected to be particularly strong. Further studies are needed to determine if allopatric populations show as many differences in vocalization structure as these sympatric populations. Factors possibly affecting interspecific differences include character convergence and divergence, and regional variations in en-

vironment. Greater Prairie-Chickens inhabit a relatively limited range of habitats whereas Sharp-tailed Grouse are more catholic in habitat preferences. A comparison of the two species could provide more information on how environments shape the structure of vocalizations.

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