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REPRODUCTIVE ISOLATING MECHANISMS AND COMMUNICATION IN
GREATER PRAIRIE CHICKENS (TYMPANUCHUS CUPIDO) AND
SHARP-TAILED GROUSE (PEDIOECETES PHASIANELLUS)

by

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Bachelor of Science, Southern Illinois University, 1971

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A Dissertation

Submitted to the Graduate Faculty

of the

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in partial fulfillment of the requirements

for the degree of

Doctor of Philosophy

Grand Forks, North Dakota

May

1979

This dissertation submitted by Donald W. Sparling, Jr. in partial fulfillment of the requirements for the Degree of Doctor of Philosophy from the University of North Dakota is hereby approved by the Faculty Advisory Committee under whom the work has been done.

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Title Reproductive Isolating Mechanisms and Communication in
Greater Prairie Chickens (*Tympanuchus cupido*) and
Sharp-tailed Grouse (*Pedioecetes phasianellus*)
Department Biology
Degree Doctor of Philosophy

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Date 12 April 1979

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ABSTRACT

Sympatric populations of greater prairie chickens (Tympanuchus cupido) and sharp-tailed grouse (Pedioecetes phasianellus) were studied between 1975 and 1978 in northwestern Minnesota for the purposes of identifying and determining the strength of reproductive isolating mechanisms between them. Major emphasis was placed on ethological mechanisms but other factors were also examined.

Approximately a fifth of the sharptail's distribution overlaps half of the prairie chicken's within North America. Within the zone of sympatry, prairie chicken populations are in small patches and may be liable to hybrid swarming, particularly with changes in land-use practices. The rate of hybridization is around 1% but may be much greater in specific areas.

Within the Minnesota study area, hybridization increased from 1-3.7% as the ratio between numbers of prairie chickens and sharptails increased. Habitat preferences and seasonal and daily patterns of activity were sufficiently similar between species to allow complete intermixing. Breeding experiments conducted in captivity showed that hybrids and backcrosses were interfertile. Thus, non-communicatory mechanisms were weak or non-existent.

Agonistic displays, including forward displays, face offs and stand offs were similar between species and probably facilitated spacing as all males held interspecifically exclusive territories on

mixed display grounds. Most epigamic behaviors such as booming displays, whoops, dancing and chिल्s were polyvalent and had many species-specific characteristics. Discriminant analysis and canonical correlation analysis were used to show that whoops and chिल्s, which were mostly epigamic, were most different between species; whines, which were polyvalent, were more similar; and cackles, the most aggressive of the 3 sets of vocalizations, were most similar between species. Interrelationships of homologous displays, as determined by cluster analyses, and by temporal occurrence of common displays, were not sufficiently different to be effective isolating mechanisms. Displays of hybrids were intermediate in form between both parental species and may have repulsed females.

Intraspecific playback experiments of vocalizations showed that prairie chicken booms, whoops and composite calls (consisting of a segment of a recording made while a prairie chicken hen visited a display ground) had agonistic functions. Prairie chicken whines also elicited significant responses but this call appeared to serve as an alarm. Sharptail males responded aggressively to gobbles, coos, cackles and alert. The functions of dancing in intermale communication were unclear.

Analyses of activity rates showed that males of both species responded more vigorously to live and taxidermist mounts of conspecific hens than to heterospecifics. Male prairie chickens, unlike sharptails, frequently courted live heterospecific females, even if doing so led to fights. Prairie chicken males reacted aggressively to sharptail coos, gobbles, cork notes and composite sounds while sharp-

tails only responded to prairie chicken cackles. Increased selectivity of sharptails for conspecific stimuli may be due to greater historical contact with confamilials and a resulting channelization of reproductive and aggressive energies to meet intraspecific competition.

During experiments conducted in captivity, females of both species strongly preferred conspecific territories and males despite being raised in mixed-species groups from hatching. F1 hybrid and backcross females were more ambiguous but may have preferred sharptail males. Precise factors determining mate choice by females were unidentified but appeared to relate to possession of a territory and to behaviors of males.

Of the mechanisms studied, behavior, particularly communication, seemed to be most important in maintaining species integrity between greater prairie chickens and sharp-tailed grouse. Based on similarities in the displays of the two species and on apparent fertility of hybrids, both grouse should be considered congeneric under Tympanuchus.

GENERAL INTRODUCTION

The study of avian reproductive isolating mechanisms has clarified many questions concerning speciation and hybridization (see, for example: Dilger, 1956; Stein, 1956; Lanyon, 1957; Johnsgard, 1961, 1963; Gill and Lanyon, 1964; Ficken and Ficken, 1968a,b,c; Anderson and Daugherty, 1974; Kroodsma, 1974a,b; Emlen, et al., 1975; Cooke and McNally, 1975; Murray and Gill, 1976; Corbin and Sibley, 1977; Hoffman et al., 1978). Most studies have shown that hybridization is a relatively rare event and when it does occur, its rate seldom exceeds a few percent of conspecific matings. Their findings have also supported Mayr's (1963) statement that ethological isolating mechanisms are the most widespread and important factors maintaining integrity of 2 closely related, sympatric species. In addition, there have been frequent indications that communication is the most important type of ethological isolating mechanism in birds.

If communication is effective in maintaining species integrity, it may operate in at least 1 of 5 ways:

1. Homologous agonistic signals may be similar between species and promote spacing among territorial individuals. This method was cited by Marler (1957) as 1 of the 2 most efficient forms of communicatory isolation. It occurs in several genera including finches (Cerduelis) (Marler, 1956), phoebes (Sayornis) (Smith, 1970), buntings (Passerina) (Emlen et al., 1975), meadowlarks (Sturnella) (Lanyon,

1957; Szijj, 1963) and waterfowl (Anas) (Delacour and Mayr, 1945; Johnsgard, 1960, 1961).

2. Epigamic signals should diverge and inhibit communication between potential heterospecific mates (Marler, 1957). Divergence can occur throughout 1 or both of the species' ranges or be limited to areas of sympatry. Frequently, identification of divergence is confounded because signals can be epigamic between sexes and agonistic within a sex. For example, Emlen et al., (1975) found that sympatric buntings learned aspects of heterospecific songs but still retained species-specific characteristics in their own songs. Ward and Ward (1974) believed a similar phenomenon occurred in chickadees (Parus); Lanyon (1957) and Szijj (1963) believed it happened in meadowlarks but Rohwer (1972) disagreed.

3. Non-homologous signals may develop in 1 species and interfere with communication; alternatively, displays may disappear from 1 species' repertoire but remain in the repertoire of the other. While this theory does not appear to have been tested previously, the situation may occur in displays which only have small segments that convey species-specificity (Falls, 1963; Emlen, 1972; Goldman, 1973; Bergmann et al., 1974; Shiovitz, 1975; Bremond, 1976). This would be most important if sympatric relatives had similar songs.

4. The perceptions of 1 species may become highly selective for conspecific signals. Selection is apt to occur if 1 species has a large distribution abutting several congeners or confamilials while the other has a restricted range. Although anurans may be highly selective for conspecific sounds (Capranica, 1965; Capranica et al.,

1973; Gerhardt, 1978), birds appear to be more general in their perceptual abilities. For example, Konishi (1970) found that while the hearing of birds was most acute near the frequency ranges of their vocalizations, it extended over much a broader spectrum. Of the 10 species tested, only house sparrows (Passer domesticus) were insensitive to the vocalizations of dark-eyed juncos (Junco hyemalis). Other, more closely related species showed complete overlap in auditory and vocal frequency ranges.

5. Although homologous displays with at least some epigamic functions may remain structurally similar because of common environmental pressures, their most important meanings (sensu Smith, 1965) may diverge. For example, a signal may have mostly agonistic denotations in a species but its homolog may have developed epigamic meanings. This mechanism has not been well-explored in the literature, probably because it is difficult to compare relative degrees of functions of particular calls between species.

In this study the nature, strength and importance of ethological isolating mechanisms between greater prairie chickens (Tympanuchus cupido) and sharp-tailed grouse (Pedioecetes phasianellus) are examined. Prairie grouse (which refers to both species collectively) share a narrow and spotty zone of sympatry in midwestern and north central United States through which hybridization usually occurs at a rate of 1-3% (Johnsgard and Wood, 1968). However, hybrid swarming swamped an island population of prairie chickens on one occasion (Lumsden, 1970). The specific objectives of this study were to:

- 1) determine why these species hybridize, particularly when

hybridization is uncommon among birds; and 2) identify factors which restrict hybridization to only a few percent.

Impetus for this study comes from 3 areas. First, prairie chickens are a declining species. The heath hen (T. c. cupido), which inhabited the eastern seaboard of the United States, became extinct in 1932. Attwater's prairie chicken (T. c. attwateri) is an endangered subspecies (USFWS, 1974), and the greater prairie chicken (T. c. pinnatus) has diminished through most of its range. Much of the decline is due to land-use practices (Hamerstrom and Hamerstrom, 1961; Johnsgard and Wood, 1968) but hybridization may pose a threat to isolated populations.

Second, the taxonomic status of prairie chickens and sharp-tails is in dispute. The American Ornithologists' Union (1957) listed them as separate genera but Short (1967) stated they were congeneric. A thorough investigation of their reproductive isolation and behavior may help determine their phylogeny and, through this, their taxonomic relationship.

Third, prairie grouse display on traditional, communal display grounds called leks and the adaptive significance of leks is a topic of great interest to behavioral ecologists. In this type of system, males defend no resource essential to females except a mating area. Pair bonds are brief or non-existent and mating can be relatively rapid. These characteristics could foster high rates of interbreeding (Sibley, 1957). In addition, because of condensed territories on leks, several males compete for channel space and they may have developed strategies that facilitate signal transmission through a very

noisy medium.

This dissertation is divided into 5 sections. The first section establishes the importance of communicatory isolating mechanisms in prairie grouse by examining other potential isolating mechanisms. The second part studies the syntactics and semantics of grouse displays as they relate to reproductive isolation and a communal social system. Sections 3 and 4 review intra- and inter-specific pragmatics of grouse signals to males and the last part examines the responses of females to con- and heterospecific males. These sections are followed by a general discussion that relates the 5 aspects of communicatory isolation to prairie grouse.

SECTION 1

POTENTIAL REPRODUCTIVE ISOLATING MECHANISMS BETWEEN GREATER PRAIRIE CHICKENS AND SHARP-TAILED GROUSE

Studies of reproductive isolating mechanisms in North American birds traditionally have centered on species with multi-purpose territories and/or monogamous pair bonds. The best known species complexes include buntings (Sibley and Short, 1959; Emlen et al., 1975), grosbeaks (Anderson and Daugherty, 1974; Kroodsma, 1974a,b), towhees (Sibley and West, 1959), orioles (Sibley and Short, 1964; Corbin and Sibley, 1977) and Vermivora warblers (Gill and Lanyon, 1964; Ficken and Ficken, 1968a,b,c; Murray and Gill, 1976). While several authors (e.g. Sibley, 1957; Johnsgard and Wood, 1968; Hjørth, 1970) have suggested looking at isolating mechanisms in species with less conventional social systems, few have done so.

Greater prairie chickens and sharp-tailed grouse are closely related tetraonids (Short, 1967) that are sympatric and hybridize in midwestern and north central United States. While hybridization is usually infrequent, it completely swamped a population of prairie chickens in at least 1 instance (Lumsden, 1970). In this complex, males are highly promiscuous, communal displayers and pair bonds (if present) are rapidly formed and dissolved. It has been suggested that these characteristics may promote hybridization (Sibley, 1957).

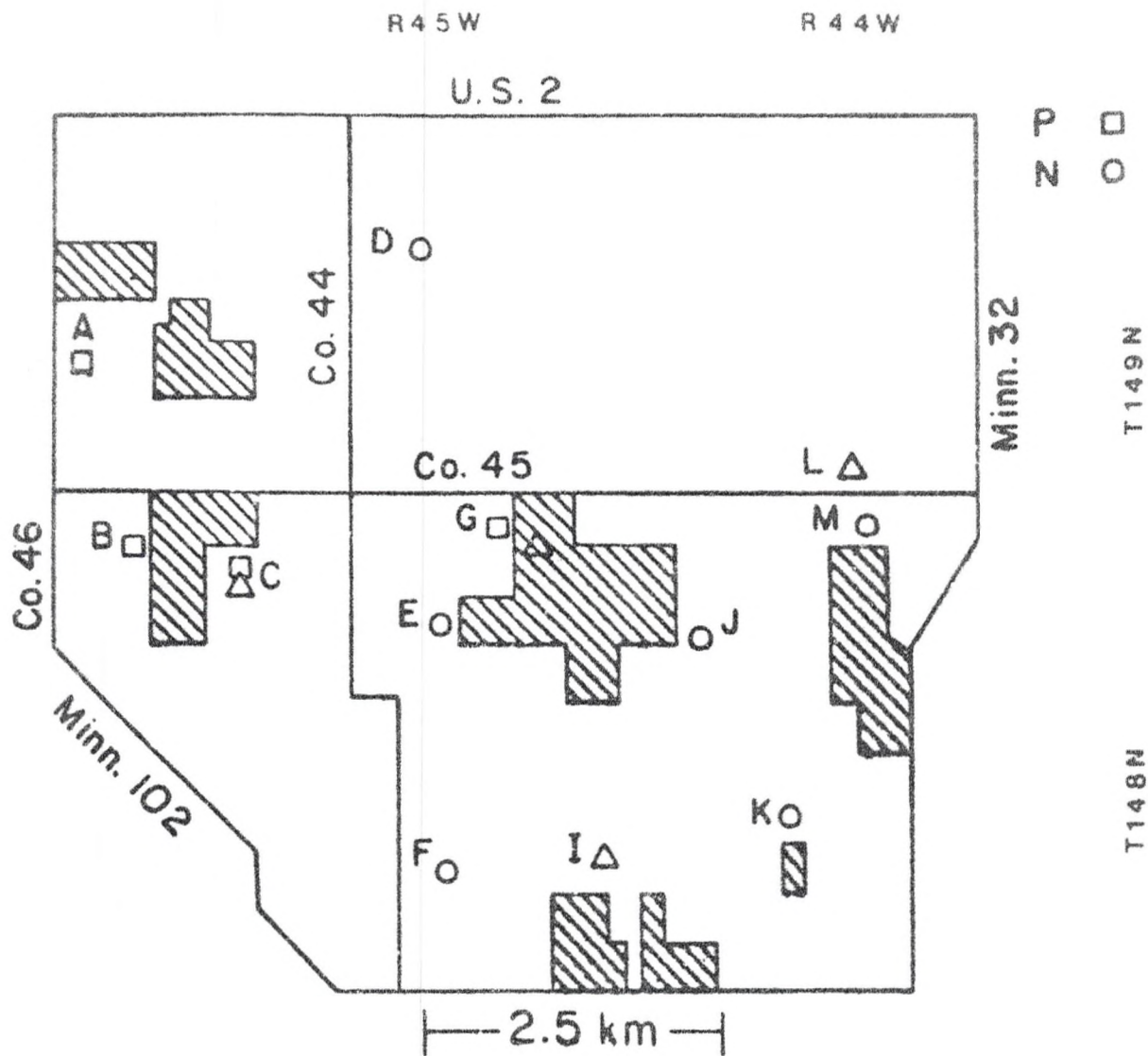
In this section, potential reproductive isolating mechanisms between greater prairie chickens and sharptails are examined. Pre-reproductive mechanisms including geographical distribution, habitat preferences and seasonal and temporal factors of breeding are emphasized. Post-reproductive mechanisms are also investigated but in less detail.

Methods and Materials

To determine the extent of geographical isolation in prairie grouse and the occurrence of hybridization, a questionnaire was sent to conservation agencies of all states and provinces having extinct or extant populations of either species. All but 2 provincial agencies responded (Appendix I). Although the extent of detailed information varied, the responses provided an estimate of the current status of these species.

Detailed information on seasonal, temporal and other aspects of mating were obtained on a study area located in Polk and Red Lake counties in northwestern Minnesota (Fig. 1). A legal and floristic description of this area is provided by Jorgenson (1977). Observations were made from blinds located on the peripheries of display grounds during spring breeding seasons of 1975-77. Limited observations were also made in 1974 by Svedarsky (personal communication) and by me in 1978. Two or 3 display grounds were visited on a rotating basis in each season to observe activities on single and mixed (i.e. with both species) species grounds. The principle objectives of data collecting were to record the number of males regularly

Figure 1. Map of study area including display grounds.
Inset shows location of study area within Minnesota. Letters near
display grounds are references to Table 1.



Display Grounds

- Prairie Chicken
- △ Sharptail
- Mixed
- ▨ Preserved Prairie



attending display grounds, the number of females visiting the grounds throughout the reproductive season and interactions between sexes.

Habitat preferences of the species were cursorily examined; additional data were provided by Svedarsky (personal communication) and Jorgenson (1977) who were concurrently studying habitat usage by prairie chickens within the area. Habitat usage has been sufficiently documented for both species (e.g. Schwartz, 1945; Ammann, 1957; Hamerstrom, 1963; Hamerstrom and Hamerstrom, 1955, 1973; Artmann, 1970; Schiller, 1973; Sisson, 1976) to allow comparison with other areas.

Postreproductive mechanisms were studied by raising grouse in captivity. All parental stock were first or second generation birds obtained as eggs from naturally occurring nest located on or within 80 km of the study area. In 1976, a first generation captive prairie chicken male and a sharptail hen were crossed. Resulting hybrids were backcrossed in 1977 to sharptails and prairie chickens. All eggs were incubated together and all downy young were housed in the same brooder until juvenile plumage was well developed. At that time, they were released into a common enclosure until mid-February when sexes were separated to prevent uncontrolled matings. In early May, pairs were housed in small (4m x 4m) pens and allowed to copulate. Resulting progeny were individually identified with wing tags and leg bands and housed together as before.

Results

Geographical Distribution

A compilation of range maps returned with questionnaires revealed that the present zone of sympatry covers portions of Wisconsin, Michigan, Minnesota, the Dakotas, Nebraska and Colorado (Fig. 2). Hybridization in most areas was less than 1% of the parental species' populations but occurred throughout the sympatric zone (Appendix I). Backcrossing occurred in at least Wisconsin and Minnesota.

Status of the Grouse Within the Study Area

For the 15 display grounds found in the Minnesota area (Fig. 1, Table 1), 3 were sharptail, 9 were prairie chicken and 3 included both species. Hybrids were found on 6 of the display grounds and they maintained territories on all but 1 sharptail dancing grounds. During the 4 years, 7 hybrid males and 1 or 2 hybrid females were observed. Four males and the 1 known hybrid female were very similar to F1 hybrids raised in captivity. The remaining males (1 each on the South and ETymp grounds) appeared to be products of sharptail x hybrid backcrossing. Known hybrids and backcrosses varied from 1 to 3% of the parental species, based on estimates of males only. Eleven of the 15 grounds were active from 1974-1978; some of these (Pantouche, Perle and Peterson) were active 10 years prior to this study. One was active in only 2 of the 4 years, while ETymp and E Pembina were active in only 1 year.

Mixed grounds, in particular, tended to have fluctuating numbers or irregularly visiting males. For example, between 1 and 5

Figure 2. Distribution of greater prairie chickens (dotted),
Attwater's prairie chickens (solid) and sharp-tailed grouse (hatched).



TABLE 1
NUMBER OF REGULARLY-ATTENDING PRAIRIE CHICKEN,
SHARPTAIL AND HYBRID MALES ON DISPLAY GROUNDS

Map ^a Symbol	Ground Name	Number of Males in Year ^b				
		1974	1975	1976	1977	1978
A	Pankratz	7,0,0	13,0,0	12,0,1	14,0,1	8,0,1
B	WTymp	2,0,1	2,0,0	4,0,0	10,1,1	4,0,0
C	ETymp	0,0,0	0,0,0	4,1,0	0,0,0	4,3,2
D	North	7,0,0	7,0,0	7,0,0	7,0,0	6,0,0
E	Lady	8,0,0	8,0,0	8,0,0	9,0,0	0,0,0
F	Peterson	14,0,0	6,0,0	5,0,0	19,0,0	4,6,0
G	Pembina	16,0,0	18,0,0	15,1,0	19,1,1	29,0,1
H	E Pembina	0,0,0	0,0,0	0,0,0	0,3,0	0,2,0
I	Liberty	0,14,0	0,14,0	0,14,0	15,14,0	35,14,0
J	South	5,0,0	9,0,0	11,0,0	12,0,0	20,0,0
K	Lee	5,0,0	9,0,0	11,0,0	12,0,0	20,0,0
	TJct	0,8,0	0,6,1	0,4,0	0,7,0	0,3,0
M	STJct	0,0,0	0,0,0	0,0,0	1,0,0	0,0,0
N	EMar	3,0,0	4,0,0	4,0,0	4,0,0	10,2,1
P	NeMar	?	2,8,0	3,8,0	0,0,0	0,0,0
Total		70,22,1	79,28,1	84,28,1	119,26,3	132,30,6

^aSymbols refer to figure 1.

^bNumbers are as follows: prairie chicken, sharptail, hybrid.

prairie chickens visited the NeMar ground between 1975 and 1976. Absence of birds in 1977 may have been due to hunters harvesting them in autumn of 1976. The WTymp and ETymp grounds were also ephemeral within and between seasons. Prairie chicken males left the ETymp ground in mid-April 1978 and, by the end of that month, remaining sharptails and hybrids moved as a group approximately 0.6 km northeast and re-established their display ground. I was especially careful not to alarm these birds, hence I do not believe that human disturbance was a factor in their movement.

Prairie chicken numbers increased during the 5-year period. Sharptails increased overall from 1974 to 1978 but decreased in 1977 due primarily to their not using the NeMar display ground. The ratio of prairie chickens to sharptails varied from 2.85 in 1975 to 4.59 in 1977. The number of hybrids increased with this ratio.

Breeding Phenology

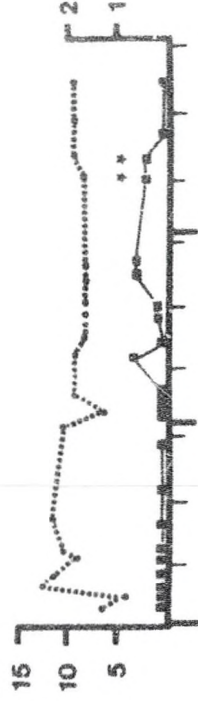
Males of both species began attending display grounds around mid-February in all 3 years. Although the number of males attending any particular ground fluctuated on a daily basis (Figs. 3-6), most males were present throughout the season. Early in the seasons, males arrived at or shortly before dawn; but, as the seasons progressed, arrival times became progressively earlier until they preceded sunrise by approximately 45 minutes (Figs. 7 and 8).

Females tended to show 2-3 distinct peaks in visitations. In 1975, peaks in sharptail hen visitations were around 9 and 20 April (Fig. 3). The first peak followed that of prairie chicken visitations by 10 days but the second peak preceded that of prairie

Figure 3. Number of sharptail males and females visiting the Tjct dancing ground and copulations observed during breeding seasons of 1975-1977.

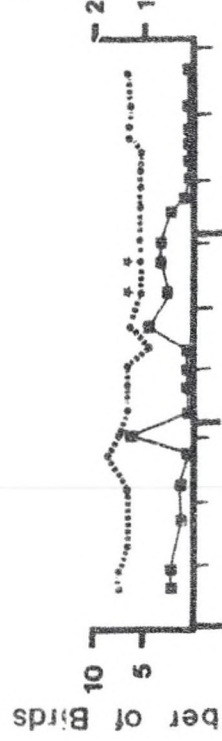
1975

* COPULATIONS
 O MALES
 — FEMALES



1976

Copulations



1977



Figure 4. Number of prairie chicken males and females visiting the Pembina booming ground and copulations observed during breeding seasons of 1975-1977.

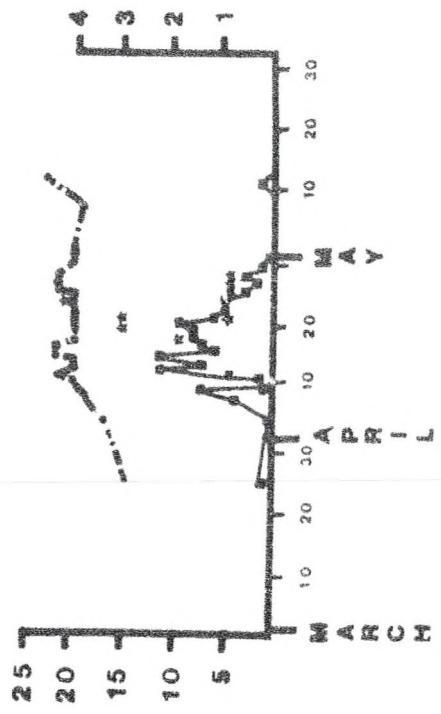
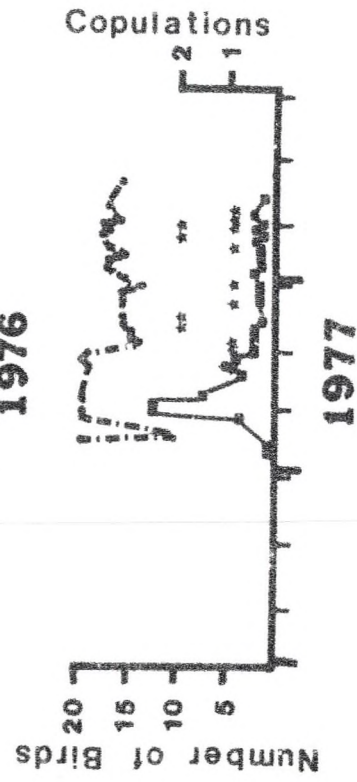
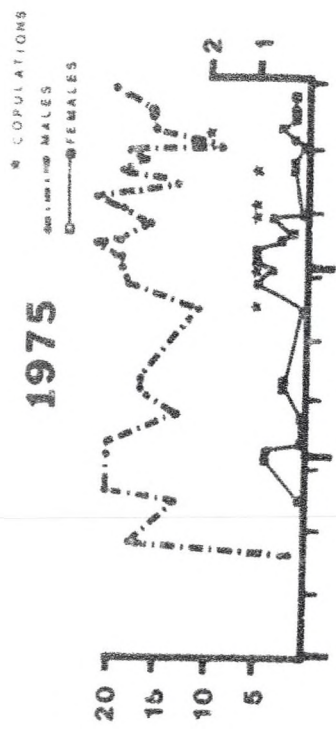


Figure 5. Number of prairie chicken males and females visiting the Pankratz booming ground and copulations observed during breeding seasons of 1975-1977.

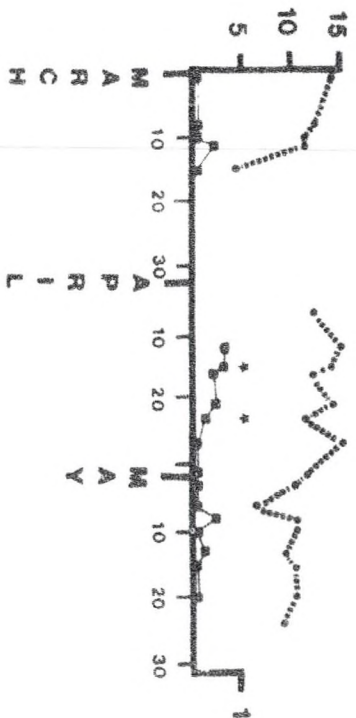
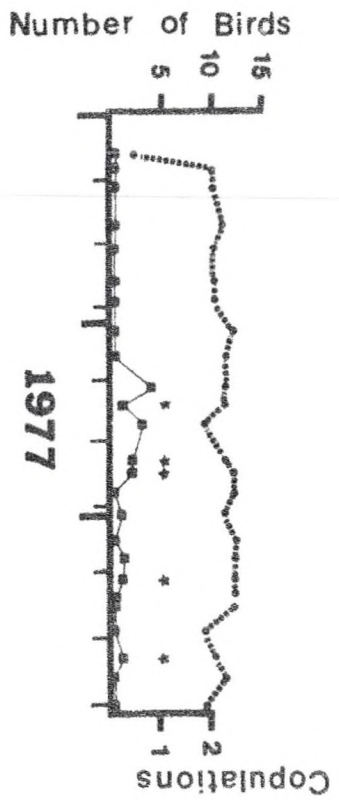
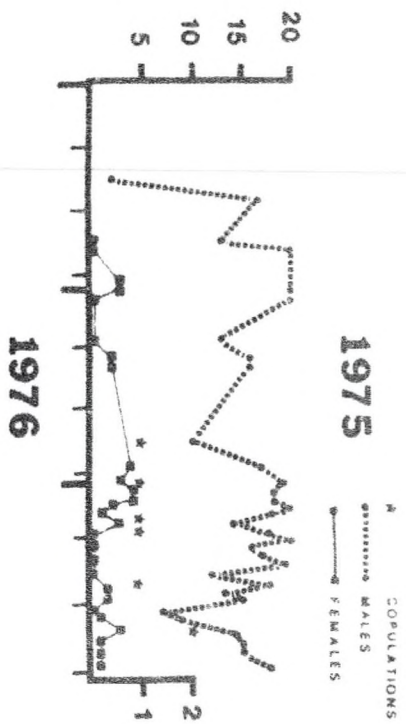


Figure 6. Number of prairie chicken and sharptail males and females visiting the NeMar mixed display ground and copulations observed during breeding seasons of 1976 and 1977.

1975

R ST COPS
 ST MALES
 ST FEMALES
 PC COPS
 PC MALES
 PC FEMALES



1976

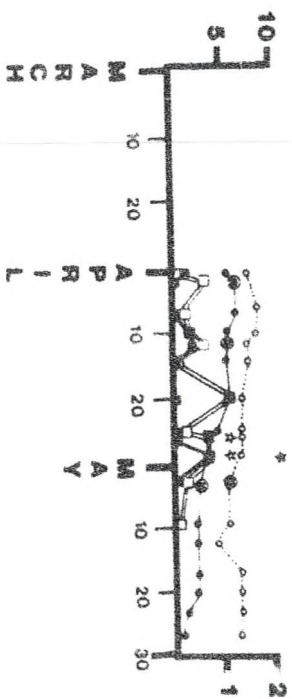


Figure 7. Arrival times of prairie chicken males on display grounds, 1975-1977. Sunrise is shown for reference. Regression equations shown in upper right corner.

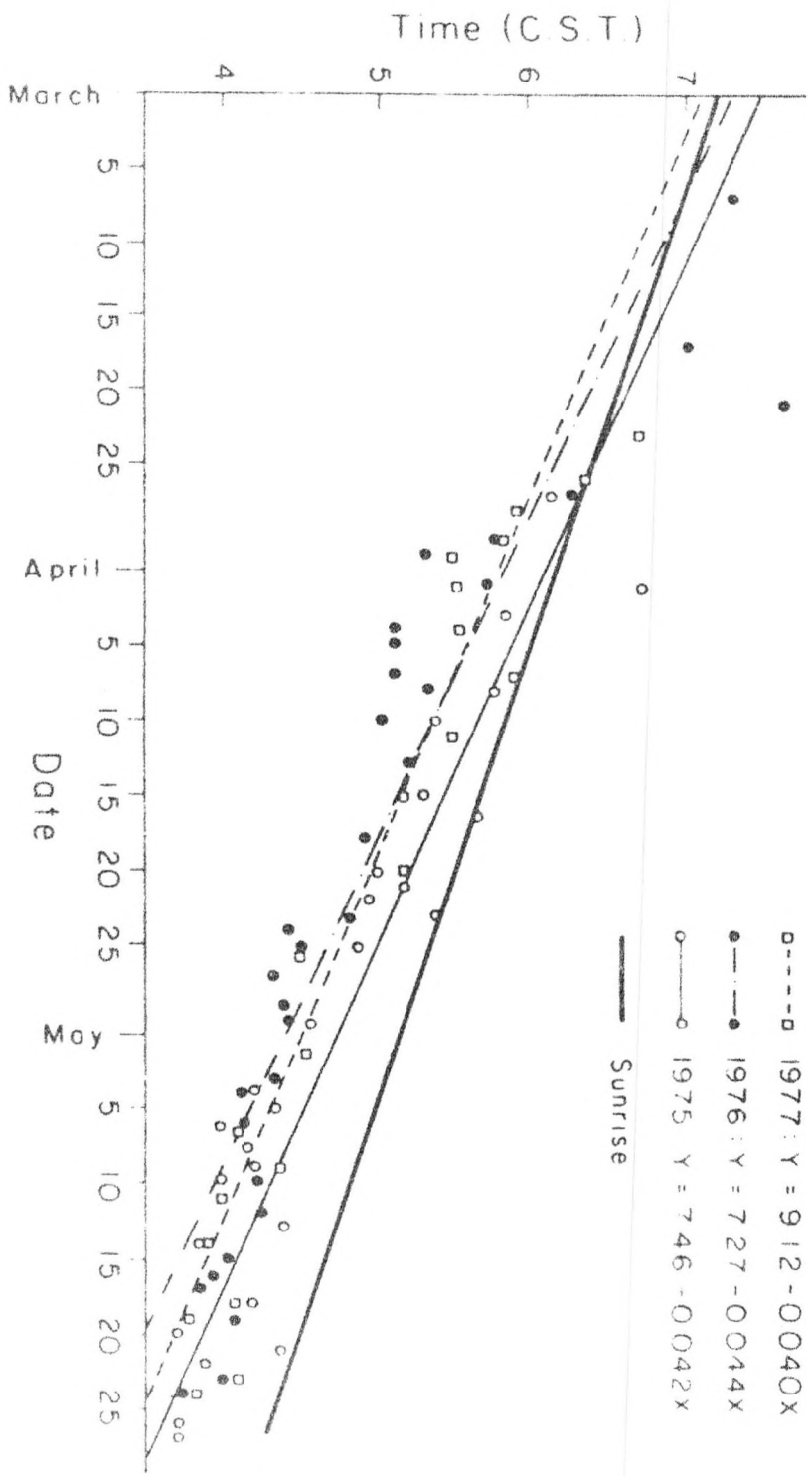
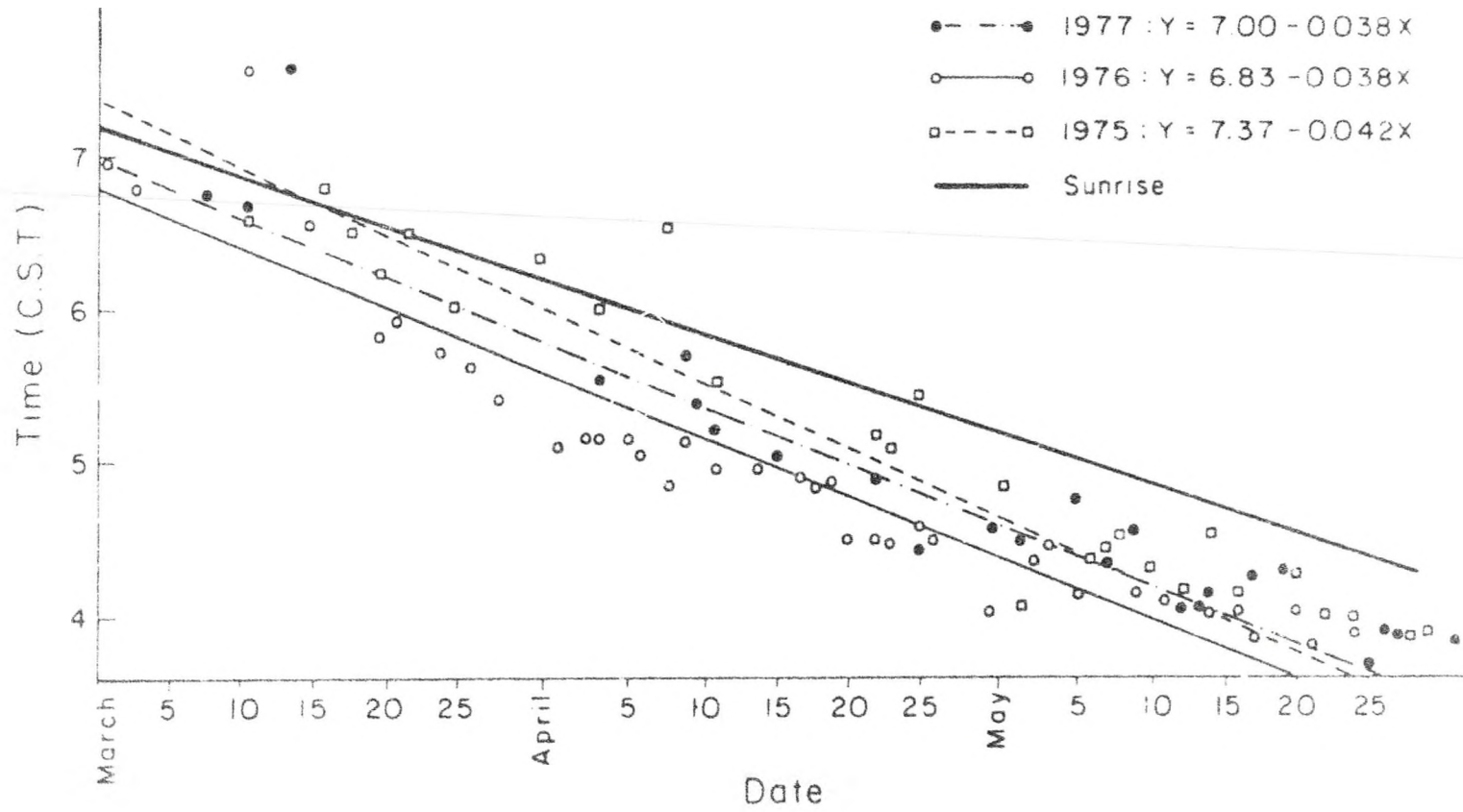


Figure 8. Arrival times of sharptail males on display grounds. Sunrise is shown for reference. Regression equations shown in upper right corner.



chicken hen on the Pembina booming ground (Fig. 4) by 7 days. In 1976, visitations of sharptail hens on the TJct dancing ground peaked on 30 March and 15 April while prairie chicken visitations peaked around 10 and 17 April on both the Pankratz (Fig. 5) and Pembina grounds. I may have missed the first peak of sharptail visitations on the NeMar display ground in 1976 (Fig. 6) due to impassable roads, but a distinct second peak occurred on 20 April. Peaks of prairie chicken visitations occurred on 10 and 27 April for this ground. In 1977, prairie chicken hens were most numerous on the Pembina ground from 12 to 18 April and this period overlapped the peak of sharptail visitations on the TJct ground. Most females of both species arrived on display grounds shortly after males and departed soon after sunrise. In general, there were no consistent interspecific differences in arrival times or peak periods of hen visitations.

Copulations tended to be most numerous shortly after the first peak of visitations. This clustering is most apparent for the Pembina display ground in 1976 and 1977 (Fig. 4) where recording behaviors of females was a primary objective. Many copulations on other grounds were not recorded but there is no obvious difference between species in the times of copulations that were noticed.

Breeding Experiments

Six females and 1 male hybrid progeny (F1's) survived to adults from the 1976 male prairie chicken x female sharptail cross. Five females were backcrossed to adult males of both species while the

hybrid male was kept with a female sharptail and the remaining hybrid. He was a listless displayer and apparently did not mate with either hen.

Fertile eggs were produced from all crosses except those with the hybrid male. Within this limited sample, fertility, hatchability and reproductive success (number of hatchlings survived/ number of eggs laid) were as high for backcrosses as for intraspecific prairie chicken but lower than sharptail matings.

Discussion

Geographical Isolation

Although the zone of sympatry has fluctuated greatly within the past century (Aldrich and Duvall, 1955; Johnsgard and Wood, 1968), it currently extends in a narrow belt from the Great Lakes to northern Nebraska. The extent of sympatry differs significantly for the 2 species. The majority of the sharptail distribution is allopatric to prairie chickens and only hybrids in the marginal southeast portion hybridize. Prairie chickens, however, have a proportionately larger area of sympatry because over 50% of their range is sympatric and only its center is allopatric. This sympatric area is in patches and may be more subject to hybrid swarming than if it was a continuous distribution of equal size. Although the distribution of sharptails may be patchier than indicated by the map, distinct pockets only occur in allopatry. Thus, sharptail populations seem less likely to be swamped.

Habitat Preferences

Differences in habitat preferences were slight or non-existent in the study area; both species occurred throughout the area and heterospecific males frequently used the same display grounds. The only apparent difference on display areas was cover height. Sharptails on the Tjct and Liberty grounds, for example, occasionally danced in tall (0.5-0.75m) grass while prairie chickens never used vegetation over a few centimeters. Six predominately prairie chicken grounds were on plowed fields. Although 3 of these (Pankratz, WTymp and Pembina) also had sharptails or hybrids, no sharptail grounds were on bare soil. Other researchers (e.g. Ammann, 1957; Johnsgard, 1973) have indicated that sharptail males tolerate higher vegetation but they also found that the differences were small. Similarly, nesting and brood rearing habitat may be similar in both species (Hamerstrom et al., 1957; Ammann, 1957; Yeatter, 1963; Westemeier, 1971; Sisson, 1976). These similarities may be due to the wider habitat tolerances of sharptails overlapping the more restricted preferences of prairie chickens.

Habitat preferences may interact with land use practices to influence the potential for hybrid swarming. Past agricultural and forestry practices have greatly altered prairie grouse distributions (Ammann, 1957; Hamerstrom and Hamerstrom, 1961; Johnsgard and Wood, 1968) and more extensive agriculture in the Great Plains in the future will depress both species. Reforestation and succession may

favor sharptails at the expense of prairie chickens, particularly at the prairie-woodland interfaces of Minnesota and Wisconsin. More importantly, land use practices may create small, isolated populations in the already patchy distributions. These pockets would be particularly vulnerable to climatic extremes and further land developments.

Temporal and Seasonal Isolation

Because there is no apparent difference between the species in circadian breeding patterns, temporal isolation is unimportant in maintaining species integrity. Similarly, the small differences in mating seasons between species negates seasonal isolation as an important factor. Even if hens of the 2 species differ by 7 to 10 days in peak periods of receptivity, males are highly active throughout the breeding season. Thus, any female entering a heterospecific's display ground may mate with a sexually active male. Other aspects of breeding such as hatching times and brood dispersal may give 1 species an advantage over the other in the zone of sympatry but the findings of other researchers (e.g. Ammann, 1957; Artmann, 1970; Hamerstrom and Hamerstrom, 1973; Schiller, 1973; Sisson, 1976) suggest that this is unlikely.

Postmating Isolation

Despite the small sample size, this study and that of McEwen et al., (1969) proved that hybrids are fertile. Further, F1 hybrids can live through at least 4 breeding seasons as did the Pankratz hybrid. While additional studies are necessary before fecundity of hybrids and fitness due to interspecific ratings can be evaluated, it is

reasonable to assume that if reduced fitness from interspecific matings does occur, females will be most affected. Males lose little by mating with a heterospecific.

Reproductive Isolation and Prairie Grouse Social Systems

Despite a predicted increase in hybridization due to brief pair bonds (Sibley, 1957), hybrid prairie grouse are relatively rare and hybridization between these species is comparable to the 1 to 7% found in meadowlarks (Szijj, 1963; Rohwer, 1972), buntings (Emlen et al., 1975) and grosbeaks in North Dakota (Kroodsmas, 1974b). It is somewhat lower than that in grosbeaks in South Dakota (Anderson and Daugherty, 1974) and Vermivora warblers (Short, 1963; Ficken and Ficken, 1968a). Clearly the rate of hybridization in prairie grouse is not comparable to the 25 to 95% found between morphs, races or incipient species such as lesser snow geese (Anser caerulescens) (Cooke et al., 1976), orioles (Sibley and Short, 1964; Corbin and Sibley, 1977) and Jamaican hummingbirds (Trochilus polytmus) (Gill et al., 1973). Thus, rapid pair bond formation and communal displaying in prairie grouse need not increase the rate of hybridization.

The unstable nature of mixed grounds may decrease reproductive fitness of males using them. Although some changes also occurred on pure grounds and some may have been related to human disturbance, Ammann (1957) found similar unstableness in mixed grounds in Michigan. Possible explanations for this unstableness include: 1) males of 1 species may be at a reproductive disadvantage on mixed grounds and quickly disperse when heterospecifics invade; or 2) males on mixed

grounds are poor in competing with conspecifics and are normally wanderers. This area needs further investigation.

When Is Hybridization Likely to Take Place?

According to Ammann (1957), hybridization will most likely occur when both species are common. In this situation, females of the more numerous species would be likely to mate interspecifically. Although Johnsgard and Wood (1968) agreed with Ammann's first premise, they believed intermating would be most likely with females of the least common species. I believe that hybridization is most likely to occur when a female has a difficult time finding a conspecific. In the 3 instances of known interspecific matings (Hamerstrom, personal communication; Sisson, 1976; Svedarsky, personal communication) a female of the rarer species copulated. In the reports by Hamerstrom and Svedarsky, it was a sharptail while Sisson saw a prairie chicken hen mate interspecifically. In this study hybrids were observed most often in the area that was dominated by prairie chickens and where Svedarsky saw an interspecific mating. Moreover, the incidence of hybridization increased with the ratio between numbers of prairie chickens and sharptails. Therefore, it appears that females of the least common species mate interspecifically and that hybridization increases as population sizes diverge. Ultimately, the number of hens may be too small to sustain a viable hybrid population and remaining hybrids will be products of introgression. This appears to have occurred on Manitoulin Island in Lake Huron (Lumsden, 1970).

Summary

Geographical, temporal, seasonal, habitat preferences and postmating reproductive isolating mechanisms were investigated in greater prairie chickens and sharp-tailed grouse. Of these mechanisms, only geographical distribution was important in keeping species apart. A substantially greater portion of the sharptails' distribution is allopatric, thus they benefit more from geographical isolation than do prairie chickens.

In general, communal displaying and rapid pair bond formation do not increase the incidence of hybridization in comparison to monogamous or other polygynous species. Hybridization is probably most likely to occur when 1 species is relatively rare and females have a difficult time finding conspecific mates. The only remaining isolating mechanisms that may be responsible for low rates of interbreeding are those involved in intra- and interspecific communication.

SECTION 2

ETHOLOGICAL ISOLATING MECHANISMS IN PRAIRIE GROUSE

I. QUANTITATIVE DESCRIPTIONS OF DISPLAYS

Communication functions as an important isolating mechanism in many avian species. For example, song serves to identify species in thrushes (Dilger, 1956), warblers (Gill and Lanyon, 1964; Murray and Gill, 1976), grosbeaks (Kroodsma, 1974a,b) and buntings (Emlen et al., 1975). Visual aspects of communication are important in lesser snow geese (Cooke and McNally, 1975), albatrosses (Fisher, 1972) and some ducks (Johnsgard, 1960, 1961, 1963). In most instances, both modalities interact to enhance species discrimination.

When communication is effective it operates most efficiently by 2 methods: 1) agonistic signals should be similar between species to facilitate spacing; and 2) courtship signals should be different and inhibit communication in this context (Marler, 1957). Although this scheme may work for displays with unambiguous meanings, polyvalent displays may not follow this simple dichotomy.

The purposes of this section are to: examine the major displays of 2 sympatric tetraonids, greater prairie chickens and sharp-tailed grouse; relate their displays to theories of ethological isolating mechanisms, particularly those of Marler (1957); and examine other theories of communication as they apply to prairie grouse. Prairie chickens and sharptails were chosen as subjects because they

share a narrow and spotty belt of sympatry in the north central and midwestern United States through which limited hybridization occurs (Johnsgard and Wood, 1968). Moreover, while geographical isolation appears important throughout most of the species' ranges; habitat preferences, temporal, seasonal and perhaps postmating mechanisms are weak or non-existent. This suggests that communication may be very important.

Another factor that led to choosing prairie grouse was that previous studies of their displays have either been merely qualitative (Grange, 1940; Schwartz, 1945); limited to only 1 species (Evans, 1961; Lumsden, 1965; Sharpe, 1968; Kermott, 1971; Kermott and Oring, 1975); or, if comparative, based on limited observations or data (Ammann, 1957; Hamerstrom and Hamerstrom, 1960; Hjorten, 1970). Thus, a quantitative comparison of their displays seems necessary to understand reproductive isolation in these species. Finally, prairie grouse are communally displaying species and an in-depth study of signals may help determine if this type of social system predisposes an animal to develop certain types of signals.

Methods and Materials

Procedures

Observations were made from blinds on display ground peripheries through the following dates: 7 February to 30 May 1975; 3 March to 29 May 1976; 18 February to 6 June 1977; and 1 April to 5 May 1978 and from vehicles throughout all years. All display grounds in 1975-1977 were located in Polk and Red Lake Counties, northwestern Minnesota, but 1 sharptail ground in Grand Forks County, North Dakota (ca. 80 km

west of the study area) was studied in 1978. Display grounds were visited on a rotating basis so that prairie chicken, sharptail and mixed grounds could be observed an average of once every 3 days. Focal areas included the Pembina and Pankratz prairie chicken grounds, NeMar, ETymp and WTymp mixed grounds and TJct and Grand Forks sharptail grounds. Each of these display areas averaged 5-25 prairie chickens and/or 4-30 sharptails per year. In addition, 7 hybrid males including 5 F1's and 2 suspected backcrosses were observed.

Observation methods included 5-minute activity samples of focal animals (Altmann, 1974) collected every 20 minutes throughout the 1975 and 1976 seasons and 15-60 minute samples collected in 1977. Films taken with a Nizo S80 super movie camera supplemented field observations and were analyzed with a film editor and stop-action projector.

Vocalizations were recorded with a Uher 4000 Report-L tape recorder at 19 cm/sec and Uher 516 omnidirectional and Sennheiser 804 ultra-unidirectional microphones. They were analyzed with a Kay Elemetrics Co. Sonagraph model 7029A set at 20-2000 or 40-4000 Hz ranges, depending on call characteristics. Narrow band sonagrams were used to measure frequency characteristics while wide band was used for temporal features. Frequency-amplitude and amplitude-time displays were used for visual but not statistical analyses.

Statistical Analyses

Besides conventional univariate statistics, multivariate procedures including discriminant analysis, canonical correlation and

cluster analyses were used on some vocalizations and activity samples to help clarify interspecific differences. Because these methods have not been widely used in studies of animal behavior, some explanation of their capabilities may be necessary. More detailed discussions are in Nie et al., (1975), Sparling and Williams (1978) and several statistical texts.

A frequent preliminary step in discriminant analysis is the use of stepwise procedures which selectively add or remove variables (in this case, call characteristics) to a predictive model based on their contribution to the variation among groups (calls). These stepwise procedures help delineate characteristics which are most important in distinguishing groups. Following these procedures, discriminant analysis reorganizes the variables into discriminant functions which can separate groups through their 'loadings' on these functions. Finally, these functions can be used to predict group membership of calls collected at a future date.

The practical difference between discriminant analysis and canonical correlation is that the latter allows the researcher to determine how characteristics distinguish calls. It does this by creating sets of variables, 1 from the calls, the other from the characteristics. Corresponding variates within these sets are in descending order of correlation and importance in variation accountability. Thus, the first few variates are most important. By plotting the loadings of calls and their characteristics on the same graph, one can determine their interrelationships. In this study discriminant analysis and canonical correlation were used on 3 sets of

homologous vocalizations: whoops and chirks; whines; and cackles.

Cluster analyses were used on activity samples taken throughout the seasons to determine the interrelationships of major displays. First, activity samples were organized into transition matrices in which, given a behavior, the frequency that another behavior followed it can be read by rows (Appendix II). Next, columns of the transition matrices were correlated or subjected to dissimilarity (distance) analysis and entered into an unweighted pair-group arithmetic averaging cluster analysis (UPGMA) (Sneath and Sokal, 1973). This procedure resulted in a pictorial representation or dendrogram of the relationships among behaviors. In this study, behaviors which are closely united are interpreted as having similar functions for they consistently occurred close to each other and in similar contexts. No assumptions concerning stationarity are implied and the transition matrices and cluster analyses cannot be used to determine sequencing.

When trying to force clusters of many different behaviors into 2-dimensional space, distortion can occur. For example, if behaviors 1, 2 and 3 were equally similar to 4 but differed among themselves, one would need a figure in 3-dimensional space to adequately show relationships among the behaviors. With more than 4 behaviors, the problem can be immense. Because clustering proceeds from right-to-left, behaviors which cluster farther to the left show greater distortions. Fortunately, an estimate of this distortion is available through cophenetic correlation values (Sneath and Sokal, 1973); high values (arbitrarily greater than 0.80) indicate low distortion.

Definitions of Terms

General terminology

1. display grounds - an area where males gather and communally display and females visit for copulation.
2. booming ground - display grounds containing prairie chickens only.
3. dancing ground - display grounds with only sharptails.
4. mixed ground - display areas containing both species.
5. lek - the social system of prairie grouse characterized by communally displaying, territorial males that do not defend any resource required by a female.
6. central males - birds whose territories are bounded on all sides by other territories.
7. peripheral males - birds having at least 1 side of their territories open.
8. prairie grouse - prairie chickens and sharptails collectively; in this dissertation the term does not include lesser prairie chickens (Tympanuchus pallidicinctus) or sage grouse (Centrocercus urophasianus).

Vocalization terminology (note: in general, the terminology for vocalizations follows conventional usage such as in Shiovitz (1975), but the following terms may need clarification):

1. note - a discrete unit of sound produced by vocalizing.
2. syllable - a unit of sound that is partially isolated by sharp discontinuities in frequency or amplitude.
3. strongest frequency - middle of a frequency band with

the darkest shading on a sonagram.

4. frequency modulation - the difference between highest and lowest levels of the strongest frequency.

Results

Description of Displays

Prairie chickens and sharptails have 10 homologous displays (Table 2), most of which are structurally similar; others differ between species or are non-homologous. The following section discusses the structure of these displays.

Prairie chicken displays

Booming displays

Booming displays were the most common visual displays in prairie chickens and were characterized by forward tilting of the body until head and nape were horizontal, elevated pinnae and tail, expanded cervical apteria and very slightly extended wings. The movements involved in this display were divided into 3 stages: 1) an introduction including forward lowering of head, elevation of pinnae and tail, wing lowering and primary spreading; 2) an intermediate stage beginning with elevation of pinnae and tail--continuing with rapid and partial sac deflation and re-inflation during the boom--and ending with a second partial deflation of sacs; and 3) a variable termination which returned the bird to an upright position. Although the display was ritualized, it varied considerably among and within individuals (Table 3), particularly in the introduction. Even more variation occurred in "booming parallel" and "listless

TABLE 2
CATALOG AND SPECIES MEMBERSHIP OF
PRAIRIE GROUSE DISPLAYS

	Prairie Chicken	Hybrid	Sharptail
Visual Displays			
Booming Displays	X	X	
Cooing Displays		X	X
Flutter Jump	X	X	X
Forward Rush	X	X	X
Running Parallel	X	X	X
Face Off	X	X	X
Stand Off	X	X	X
Nuptial Bow	X	?	X
Upright Alert	X	X	X
Dancing			X
Stamping	X	X	
Acoustical Displays			
Boom	X		
Coom		X	
Coo		X	X
Gobble		X	X
Cork Notes			X
Chilks		X	X
Whoops	X	X	
Cluck	X	X	X
Whine	X	X	X
Cackle	X	X	X

TABLE 3
TEMPORAL AND POSTURAL VARIATION IN
PRAIRIE CHICKEN BOOMING DISPLAYS

Character ^a		Male				
		One	Two	Three	Four	Five
1. Stamp	\bar{X}	1.13	3.05	2.43	2.97	2.29
	SD	0.18	1.81	1.43	1.18	1.34
	CV	16.0	59.2	58.8	39.6	58.5
2. Sacs 1	\bar{X}	0.08	0.20	0.40	0.55	0.71
	SD	0.05	0.28	0.46	0.32	0.39
	CV	55.9	136.6	116.0	57.7	54.9
3. Sacs 2	\bar{X}	0.57	0.43	0.78	1.54	2.13
	SD	0.21	0.40	0.40	0.68	0.57
	CV	37.4	94.6	50.9	44.1	26.9
4. Sacs 3	\bar{X}	0.56	0.29	0.20	0.14	0.19
	SD	0.21	0.33	0.12	0.09	0.20
	CV	37.9	114.0	59.5	67.5	105.0
5. Sacs 4	\bar{X}	0.23	0.23	0.33	1.05	1.62
	SD	0.15	0.24	0.27	0.67	0.55
	CV	68.0	102.0	82.2	64.2	34.3
6. Sacs 5	\bar{X}	0.78	1.59	0.43	0.44	0.53
	SD	0.26	0.50	0.19	0.17	0.19
	CV	33.3	71.4	45.8	37.2	35.1
7. Head	\bar{X}	0.78	1.59	0.73	0.76	1.39
	SD	0.32	0.45	0.63	0.55	1.10
	CV	40.4	28.2	85.9	72.3	79.2
8. Walk	\bar{X}	1.00	2.09	0.31	0.37	0.52
	SD	0.39	1.41	0.32	0.29	0.58
	CV	38.9	67.4	105.7	78.7	111.1

TABLE 3--Continued

Character		Male				
		One	Two	Three	Four	Five
9. Walk	\bar{X}	2.70	3.43	1.45	1.56	2.53
	SD	0.42	1.06	0.77	0.48	1.13
	CV	11.6	31.1	53.1	30.9	44.5
10. Walk	\bar{X}	2.13	3.22	0.64	0.63	0.86
	SD	0.31	1.12	0.59	0.54	0.81
	CV	14.6	34.7	91.9	88.5	94.0
11. Pinnae		165 ⁰	165 ⁰	165 ⁰	165 ⁰	165 ⁰
12. Tail		95 ⁰	100 ⁰	130 ⁰	125 ⁰	130 ⁰
N ^c		9	7	12	10	15

^aDefinition of characters: 1) duration of stamping; 2) time between end of stamping and first inflation of sacs; 3) total time sacs inflated; 4) duration of first inflation; 5) duration of second inflation; 6) time between first and second inflation; 7) time between second inflation and head elevation; 8) time between head raising and walking; 9) time between first inflation and walking; 10) time between sac deflation and walking (all temporal characters in sec); 11) maximum erection of pinnae with pinnae flat on neck used as 0⁰ reference; 12) maximum erection of tail with horizontal used as 0⁰ reference.

^bCV = coefficient of variation = $(SD / \bar{X}) \times 100$.

^cN = number of displays analyzed.

tooting" (Hjorth, 1970).

Booming displays occurred most frequently and were most intense when females were likely to be present. They were less vigorous during territorial disputes or while a male was alone in the center of his territory. Hybrids gave "cooming" displays which were similar in form and context to booming displays. Although many components including pinnae elevation, stamping and sac inflation were in displays of prairie chicken and hybrids, hybrids had several elements that were intermediate between booming and sharptail dancing. For example, the Pankratz hybrid stamped longer, elevated his wings higher and occasionally bowed lower than prairie chickens (Table 4).

Stamping

In stamping, acoustical and visual signals were produced by treading the ground. Stamping seldom occurred alone and usually preceded booms and whoops. It was not analyzed in detail for Hjorth (1970) adequately described it.

Boom

Booms were loud, resonant, single vocalizations of low frequency and simple harmonic structure (Fig. 9.A1, Table 5). They were usually composed of 3 syllables with the first 2 having greatest amplitude. A few calls had the first syllable divided into 2 or 3 distinct notes. These were most common in late mornings or seasons and characterized individuals.

Booms occurred in a variety of contexts including territorial conflicts ('booming parallel') and during courtship. Their loudest,

TABLE 4

TEMPORAL AND POSTURAL CHARACTERISTICS OF
PANKRATZ HYBRID 'COOMING' DISPLAYS

Character ^a		
1. Stamping	\bar{X}	1.57
	SD	0.61
	CV	38.9
2. Stamping to Inflation	\bar{X}	0.15
	SD	0.06
	CV	40.7
3. Inflation to Sound	\bar{X}	0.21
	SD	0.08
	CV	39.2
4. Wing Lowering	\bar{X}	0.20
	SD	0.04
	CV	20.1
5. Deflation to Terminal	\bar{X}	0.09
	SD	0.03
	CV	35.9
6. Duration of Ending	\bar{X}	0.27
	SD	0.16
	CV	59.0
7. Inflation to End	\bar{X}	0.54
	SD	0.21
	CV	39.0
8. First Act		Head extension (4)
9. Head Bow to Inflation	\bar{X}	0.05
	SD	0.00
	CV	0.00

TABLE 4--Continued

Character			
10. Duration of Inflation	\bar{X}	0.18	
	SD	0.05	
	CV	26.7	
11. Wing Return	\bar{X}	0.17	
	SD	0.12	
	CV	68.4	
12. Pinnae		149 ⁰ -165 ⁰	
13. Tail Erection		25 ⁰ -95 ⁰	
14. Wing Angle		20 ⁰ -40 ⁰	down from horizontal
		40 ⁰ -50 ⁰	back from vertical
15. Angle of Back		5 ⁰ -0 ⁰	tilted forwards
N		8	

^aDefinition of characters: 1) duration of stamping; 2) time between end of stamping and inflation of sacs; 3) time between sac inflation and 'coom'; 4) duration of wing lowering and primary spreading; 5) time between sac deflation and head elevation; 6) time between head raising and walking; 7) time between sac inflation and walking; 8) first act - sac inflation or head lowering; 9) time between sac inflation and head bowing; 10) duration of sac inflation; 11) duration of wing elevation (all temporal characteristics in sec); 12) maximum erection of pinnae; 13) maximum erection of tail; 14) angle of wings from vertical; 15) angle of back below horizontal.

Figure 9 Sound spectrograms of some prairie grouse vocalizations. A1 - prairie chicken boom; A2 - sharptail coos; B1 - WTymp hybrid coom; B2 - WTymp hybrid coo; C1 - prairie chicken whoop; C2 - WTymp hybrid whoop; C3 - WTymp chilk; C4 - sharptail chilk.

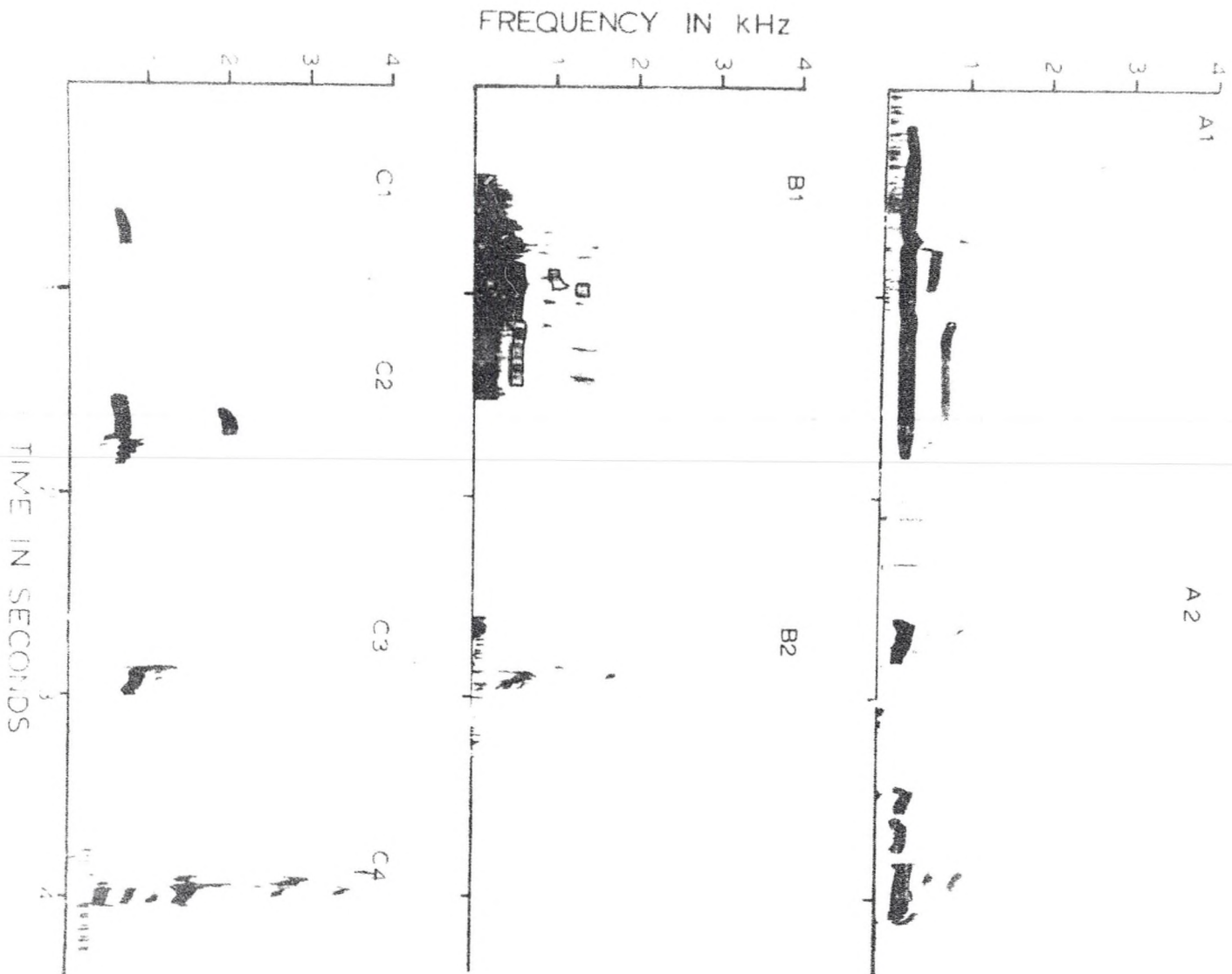


TABLE 5
CHARACTERISTICS OF RANDOMLY SELECTED
BOOMS AND COOS

		Prairie Chicken Booms	Sharptail Coos	WTymp Hybrid Coos
Number of Notes or Syllables	\bar{X} SD	2.73 0.89	21.71 39.82	1.50 0.71
Duration of:				
Syllable 1	\bar{X} SD	0.67 0.46		
Syllable 2	\bar{X} SD	0.69 1.20		
Syllable 3	\bar{X} SD	0.30 0.36		
Call	\bar{X} SD	2.73 0.49	0.22 0.08	0.33 0.03
Internote Intervals	\bar{X} SD	6.64 3.88	3.40 4.09	1.58 2.24
Frequency Characteristics:				
Strongest Frequency	\bar{X} SD	268 17	297 54	342 14
Highest Frequency	\bar{X} SD	314 25	297 54	342 14
Frequency Modulation	\bar{X} SD	48 18	81 4	92 14
N ^a		128	306	4

^aSample sizes refer to number of samples taken. Eleven prairie chickens, 11 sharptails and 1 hybrid were analyzed. Temporal characteristics in seconds, frequency characteristics in Hertz.

most intense versions, however, were given when females were present.

Hybrids gave aberrant forms of this call during similar situations (Fig. 9.B1). These vocalizations were very soft and lacked resonance. They were not analyzed further because few could be recorded.

Whoops

These slightly repeated vocalizations had moderate lengths, high (for prairie grouse) frequencies, simple harmonic structure and variable modulation (Fig. 9.C1, Table 6). They were often given when hens were on a booming ground, particularly when in a male's territory.

Four F1 hybrid males whooped; 2 were analyzed in detail (Fig. 9.C2, Table 6). Their calls differed from those of prairie chickens in internote interval, total duration and note duration. In addition, whoops of the WTymp hybrid differed from those of prairie chickens and the Pankratii hybrid in lowest and strongest frequencies

Sharptail displays

Dancing

In dancing, visual and acoustical signals were combined into highly characteristic displays which could be divided into active and passive phases. During active phases, males elevated their wings to horizontal, leaned forward so that nape and back formed a line slightly below horizontal, erected their tails and produced loud puttering sounds by synchronizing foot stamping and tail-rattling. Passive phases were characterized by variable forms of the

TABLE 6
CHARACTERISTICS OF RANDOMLY SELECTED
WHOOPS AND CHILKS

		Prairie Chicken Whoops	Sharptail Chilks	WTymp Hybrid Whoops	WTymp Hybrid Chilks	Pankratz Hybrid Whoops
Number of Notes	\bar{X} SD	1.05 0.22	1.91 1.09	1.33 0.65	1.12 0.35	1.50 0.92
Note Duration	\bar{X} SD	0.27 0.10	0.09 0.04	0.42 0.10	0.23 0.05	0.48 0.22
Internote Interval	\bar{X} SD	0.01 0.05	0.07 0.11	0.14 0.30	0.13 0.38	0.06 0.11
Total Duration	\bar{X} SD	0.30 0.14	0.28 0.29	0.71 0.63	0.38 0.42	0.70 0.37
Lowest Frequency	\bar{X} SD	465 117	889 340	729 132	380 95	462 85
Strongest Frequency	\bar{X} SD	622 134	1401 429	767 97	926 49	677 339
Highest Frequency	\bar{X} SD	890 436	2487 1021	2167 1055	2504 1268	1451 395
Frequency Modulation	\bar{X} SD	119 75	184 158	249 115	306 149	203 73
^a N		41	43	12	8	8

^a
N = number of sequences analyzed. Nine prairie chickens, and 12 sharptails were analysed. Hybrids represent one individual each. Temporal characteristics in seconds, frequency characteristics in Hertz.

forward postures: wings could be elevated or folded and the back could be at or slightly above horizontal.

Variation in most of the temporal characteristics of dancing, especially duration of passive phases, was high but posturing was slightly more stereotyped (Table 7). Peripheral and central males differed only in that peripherals took longer to turn and lower their wings and were less variable in some other components.

Dancing occurred in a variety of contexts such as when males forward rushed each other, ran parallel or attacked to interrupt mating. The most intense displays as well as synchronization of males occurred when females were present. Synchronization was not a result of any particular individual because male and female movements were unrelated and any male, regardless of status, could begin the active phase of dancing.

Chilks

Chilks were loud, temporally variable vocalizations that formed a continuum from squeaks to longer 'chas' (Table 6). Although pitch correlated with note duration, all forms of chilks were harmonically complex and had sharp breaks in frequency (Fig. 9.C4). These calls occurred during and shortly following dancing. Squeaks were most common in agonistic situations and occasionally occurred apart from dancing.

Among hybrids, only the WTymp bird chilked (Fig. 9.C3, Table 6). The calls of this individual were longer and had lower frequencies and greater modulation than those of sharptails. His chilks

TABLE 7
TEMPORAL AND POSTURAL VARIATION IN
SHARPTAIL DANCING DISPLAYS

Character ^a	Male Identification					
	One	Two	Three	Four	Five ^b	Six ^b
1. Quiet	\bar{X} 3.93 SD 2.18 CV 55.5	4.06 4.21 103.9	1.94 2.40 123.8	3.23 3.23 96.6	3.29 2.71 82.2	4.37 3.98 91.0
2. Wing 1	\bar{X} 0.27 SD 0.26 CV 96.3	0.47 0.25 53.8	0.40 0.12 29.1	0.53 0.40 76.0	0.42 0.20 46.8	0.52 0.24 46.3
3. Stamp	\bar{X} 2.47 SD 0.87 CV 35.2	3.51 1.56 44.4	2.87 1.17 40.7	1.96 0.84 43.1	2.73 0.80 29.1	2.13 1.21 56.8
4. Turn	\bar{X} 0.98 SD 0.66 CV 57.7	0.29 0.27 90.0	0.37 0.43 117.2	0.39 0.33 85.3	0.82 0.51 61.6	0.64 0.55 84.9
5. Wing 2	\bar{X} 0.52 SD 0.30 CV 57.6	0.19 0.08 40.7	0.25 0.12 46.8	0.22 0.22 100.2	0.43 0.16 37.9	0.42 0.14 33.9
6. Head Angle	20°	20°	20°	20°	20°	20°
7. Wing Angle	20°	20°	20°	20°	20°	20°
N	11	24	9	19	9	25

^aDefinition of characters: 1) duration of quiet phase; 2) duration of wing elevation; 3) duration of stamping; 4) time between initiation of stamping and first turn; 5) duration of wing lowering; 6) angle formed by head during active phase, horizontal used as 0° reference; 7) angle formed by wings below horizontal during active phase. All time measurements in seconds.

^bPeripheral males.

and whoops differed primarily in note and total duration.

Cork Notes

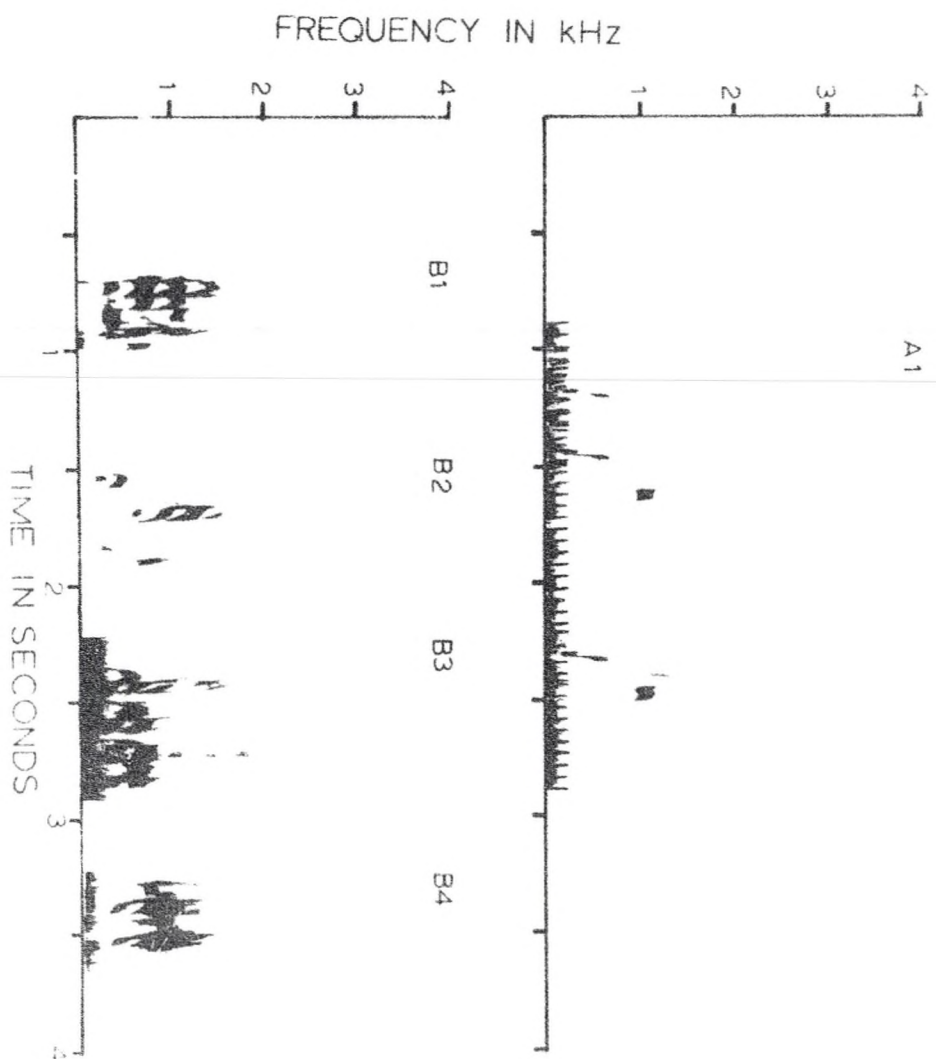
Cork notes were soft, frequently repeated calls which were composed of 1 to 3 sounds (Fig. 10.A1). The 2 most frequently occurring components were a low frequency, highly modulated introductory note which sounded like a cork popping from a bottle and a higher, pure tone reminiscent of a pebble plinking in water. A third, very brief element occasionally occurred between these 2 and was probably produced by rapid lateral flicking of rectrices. The 2 vocalizations could occur separately (see the first note of Fig. 10.A1), but it is not known if the tail-popping sound was independent for it would be easily missed on a spectrogram. These sounds were virtually limited to intense dancing when females were present.

Coos

These moderately-long, low vocalizations (Fig. 9.A2, Table 5) are homologous to prairie chicken booms but were not as loud or resonant. They were associated with visual cooing displays which were very similar to forward postures except that air sacs were inflated during vocalization.

Coos were given by males in the center of their territories and more often by peripheral than by central birds. They occurred in contexts including territorial disputes, when territorial intrusion was likely and spontaneously, but they were infrequent when females were present.

Figure 10. Sound spectrograms of cork notes and gobbles.
A1 - 3 cork notes; B1, B2 - 2 gobbles from 2 sharptail males;
B3 - gobble from Pankratz hybrid male; B4 - gobble of WTymp hybrid.



Gobbles

Gobbles consisted of 3 to 5 notes separated by very short intervals. They had very intricate frequency structures (Fig. 10, Table 8). Characteristics of the calls could be used to distinguish individuals (Table 9) and preliminary discriminant analysis classified birds with over 80% reliability based on number of notes. Gobbles occurred in agonistic situations. They were usually given by central males on the edges of their territories where the chances of overt aggression were high.

All male hybrids gobbled. One that occupied the Pankratz booming ground gave gobbles that differed from those of sharptails in the duration of notes, total duration and strongest frequency of first note (Table 8, Fig. 10). Another hybrid male on a mixed ground had gobbles equally different from the first hybrid and from sharptails (Fig. 10.B4). Hybrids gobbled in the same contexts as sharptails.

Displays common to both species

Flutter jumping

This display was characterized by a forward jump into the air, wing fluttering and slight forward flight. Flutter jumps differed among the species and hybrids in that sharptails jumped less frequently, had longer jumps that developed into flutter flights and were silent. Prairie chickens and hybrids whined and cackled when flutter jumping.

TABLE 8
CHARACTERISTICS OF GOBBLES

		Sharptail Gobblers	Pankratz Hybrid Gobblers
Number of Notes	\bar{X} SD	3.83 1.16	4.33 0.51
Duration of Notes			
Note 1	\bar{X} SD	0.06 0.03	0.12 0.02
Note 2	\bar{X} SD	0.06 0.02	0.12 0.03
Note 3	\bar{X} SD	0.04 0.02	0.08 0.02
Note 4	\bar{X} SD	0.02 0.03	0.11 0.03
Internote Intervals			
Interval 1	\bar{X} SD	0.03 0.02	0.03 0.02
Interval 2	\bar{X} SD	0.03 0.02	0.02 0.01
Interval 3	\bar{X} SD	0.02 0.02	0.02 0.02
Total Duration	\bar{X} SD	0.29 0.10	0.54 0.06

TABLE 8--Continued

Frequency Characteristics of First Note			
Number of	\bar{X}	4.12	3.00
Freq. Bands	SD	1.19	0.89
Lowest	\bar{X}	252	283
Frequency	SD	136	23
Strongest	\bar{X}	1213	554
Frequency	SD	1721	66
Highest	\bar{X}	1240	1287
Frequency	SD	989	466
Frequency	\bar{X}	302	223
Modulation	SD	91	823
N^a		142	6

^aSample size refers to number of gobblers analyzed. A total of eight sharptails and one hybrid were used in the analysis.

TABLE 9
CHARACTERISTICS OF GOBBLES FROM INDIVIDUALS

		Bird Identification			
Character		TJct 1	TJct 3	TJct 5	TJct 8
Number of Notes	\bar{X}	3.25	3.44	4.05	4.88
	SD	0.45	0.89	1.08	1.45
Duration of Notes					
Note 1	\bar{X}	0.06	0.05	0.05	0.06
	SD	0.02	0.02	0.03	0.01
Note 2	\bar{X}	0.06	0.05	0.06	0.06
	SD	0.01	0.01	0.01	0.01
Note 3	\bar{X}	0.03	0.03	0.04	0.04
	SD	0.01	0.02	0.02	0.02
Note 4	\bar{X}	0.01	0.01	0.02	0.03
	SD	0.01	0.01	0.02	0.02
Note 5	\bar{X}	0.00	0.01	0.01	0.02
	SD		0.01	0.02	0.02
Internote Interval					
Interval 1	\bar{X}	0.04	0.04	0.03	0.02
	SD	0.01	0.03	0.02	0.01
Interval 2	\bar{X}	0.03	0.02	0.03	0.02
	SD	0.01	0.03	0.02	0.01
Interval 3	\bar{X}	0.01	0.01	0.02	0.03
	SD	0.02	0.02	0.02	0.02
Interval 4	\bar{X}	0.00	0.00	0.01	0.00
	SD	0.00	0.01	0.02	0.03

TABLE 9--Continued

Total Duration	\bar{X} SD	0.23 0.03	0.24 0.07	0.28 0.08	0.36 0.10
Frequency Characteristics of First Note					
Number of Freq. Bands	\bar{X} SD	2.58 0.67	4.19 0.83	4.83 1.12	4.84 0.80
Lowest Frequency	\bar{X} SD	294 48	278 51	150 133	288 155
Strongest Frequency	\bar{X} SD	479 134	704 85	734 302	755 217
Highest Frequency	\bar{X} SD	801 154	1187 190	1352 1558	1262 218
Frequency Modulation	\bar{X} SD	74 58	101 60	533 1475	81 57
^a N		12	16	42	25

^a Sample size refers to number of sequences analyzed. Temporal characteristics are in seconds, frequency characteristics in Hertz.

Nuptial bows

At times of high sexual excitement, males stood before hens and bowed low, sometimes touching their bills to the ground. During these bows, sharptails extended and undulated their wings and uttered a soft "crooning" (Lumsden, 1965). The display was not observed in hybrids, possibly because of its infrequency.

Forward displays

Three graded displays including the forward posture, forward rushing and running parallel stemmed from a common initial position, the forward, (Hjorth, 1970). All occurred during territorial conflicts. Forward displays differed in the 2 species in that sharptails frequently elevated their wings 60° to 90° from vertical and kept their heads low. Prairie chickens had higher heads and held their wings at their sides. The Pankratz hybrid gave forward displays that were nearly indistinguishable from those of prairie chickens but the WTymp hybrid switched between folded and extended-wing forward rushes, depending if it interacted with prairie chickens or sharptails.

Face offs and stand offs

These visual displays occurred when 2 males confronted each other at territorial borders, sat (face off) or stood (stand off) and faced each other. Sharptails and hybrids usually squatted lower than prairie chickens and sharptails occasionally faced off with wings extended on the ground.

Whines and cackles

Whines and cackles were invariably mixed but could be distinguished within a species by note duration and by lowest and strongest frequencies (Tables 10 and 11, Fig. 11). The 2 calls were similar in structure among both species and hybrids but differed in context between prairie chickens and sharptails. The whines and cackles of prairie chickens and hybrids, for instance, frequently accompanied face offs, fighting and flutter jumps and occurred when potential danger such as a raptor was near. Sharptails, however, only gave the calls during face offs and overt fighting. Sharptails sometimes gave a cackle-like call when flushed but this call differed from that described here in pitch and internote interval.

Overt fighting

Territorial conflicts often developed into overt fighting including bill and head thrusting, feather pulling, pouncing and kicking. Fighting was identical in both species and hybrids. Interspecific recognition of aggression was evident in that males gave corresponding face offs, forward rushes and running parallels and males held mutually exclusive territories on all mixed grounds (Figs. 12 to 14).

Other behaviors

During quiet periods such as late mornings or seasons, prairie grouse stood, ran, walked, crouched or gave various comfort movements. While some of these behaviors may have been redirected aggression or displacement behaviors, most were non-communicatory. Alarmed birds

TABLE 10
CHARACTERISTICS OF RANDOMLY SELECTED WHINES

		Prairie Chicken	Sharptail	Pankratz Hybrid	WTymp Hybrid
Number of Notes	\bar{X} SD	9.24 2.10	4.65 2.98	5.54 1.86	16.40 9.14
Note Duration	\bar{X} SD	0.19 0.06	0.37 0.13	0.16 0.05	0.27 0.07
Internote Interval	\bar{X} SD	0.20 0.09	0.34 0.24	0.28 0.24	0.23 0.11
Total Duration	\bar{X} SD	4.63 6.16	4.52 12.58	3.54 5.01	6.93 3.54
Number of Freq. Bands	\bar{X} SD	3.86 0.88	5.43 9.59	3.58 0.86	2.88 0.50
Lowest Frequency	\bar{X} SD	429 288	367 126	365 139	455 66
Strongest Frequency	\bar{X} SD	989 542	867 1208	836 502	831 131
Highest Frequency	\bar{X} SD	2033 405	1211 295	1938 470	1333 301
Frequency Modulation	\bar{X} SD	281 155	238 273	232 110	106 62
^a N		42	49	11	10

^a Sample size refers to number of sequences analyzed. Nine prairie chickens, 14 sharptails and two hybrids were analyzed. All temporal characteristics in seconds, frequency characteristics in Hertz.

TABLE 11
CHARACTERISTICS OF RANDOMLY
SELECTED CACKLES

		Prairie Chicken	Sharptail	Pankratz Hybrid	WTymp Hybrid
Number of Notes	\bar{X} SD	9.92 7.25	25.72 26.53	7.67 4.73	46.25 2.63
Note Duration	\bar{X} SD	0.05 0.01	0.08 0.12	0.04 0.01	0.09 0.005
Internote Interval	\bar{X} SD	0.08 0.02	0. 0.1	0.05 0.01	0.12 0.01
Total Duration	\bar{X} SD	1.25 1.01	4.31 7.70	3.72 0.36	3.95 0.62
Number of Freq. Bands	\bar{X} SD	4.59 1.39	4.39 5.59	3.72 0.62	3.95 0.09
Lowest Frequency	\bar{X} SD	379 239	574 964	404 222	337 11
Strongest Frequency	\bar{X} SD	760 480	745 241	1012 306	811 122
Highest Frequency	\bar{X} SD	1665 455	1365 859	1354 310	1217 67
Frequency Modulation	\bar{X} SD	100 75	196 374	93 20	53 86
^a N		72	29	4	4

^a Sample size refers to number of sequences analyzed. Ten prairie chickens, nine sharptails and two hybrids were analyzed. Temporal characteristics in seconds, frequency characteristics in Hertz.

Figure 11. Sound spectrograms of prairie grouse whines and cackles. A1 - prairie chicken whines; A2 - Pankratz hybrid whines; A3 - sharptail whines; B1 - prairie chicken cackles; B2 - Pankratz hybrid cackles; B3 - sharptail cackles.

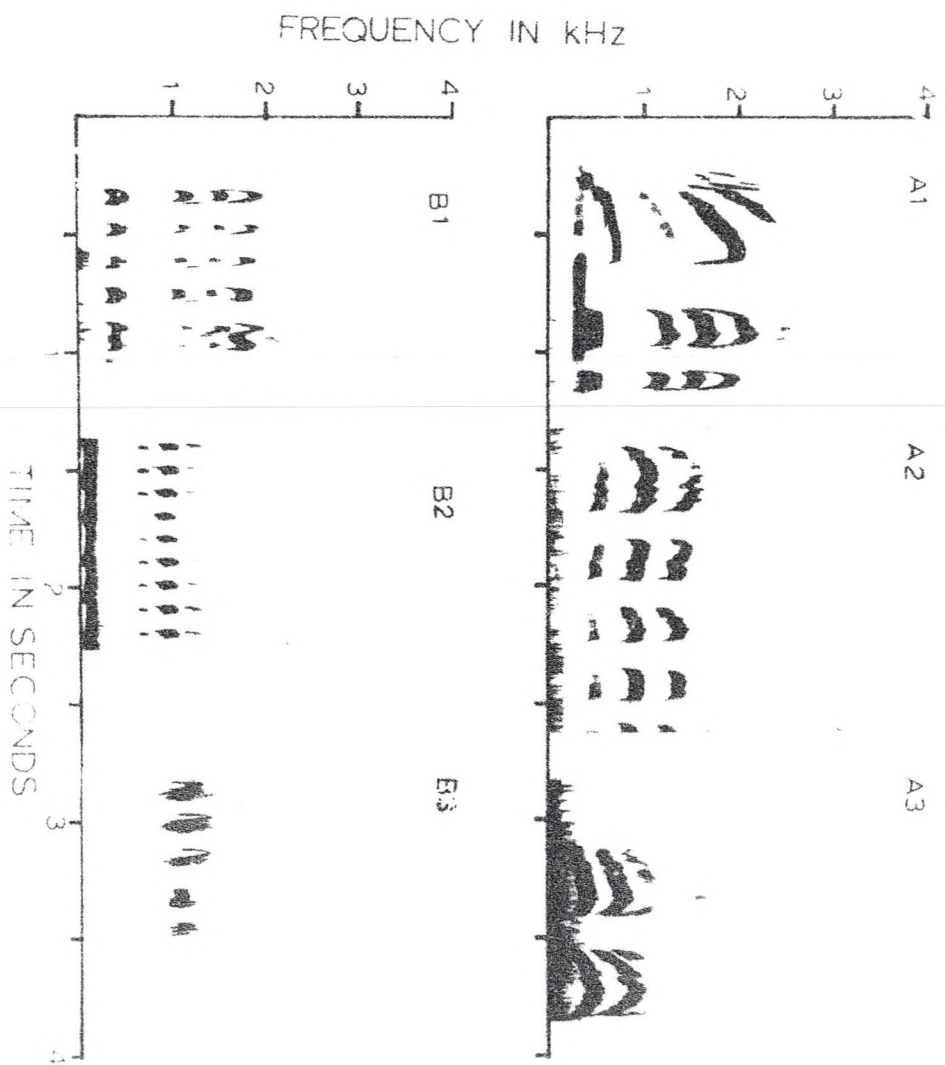
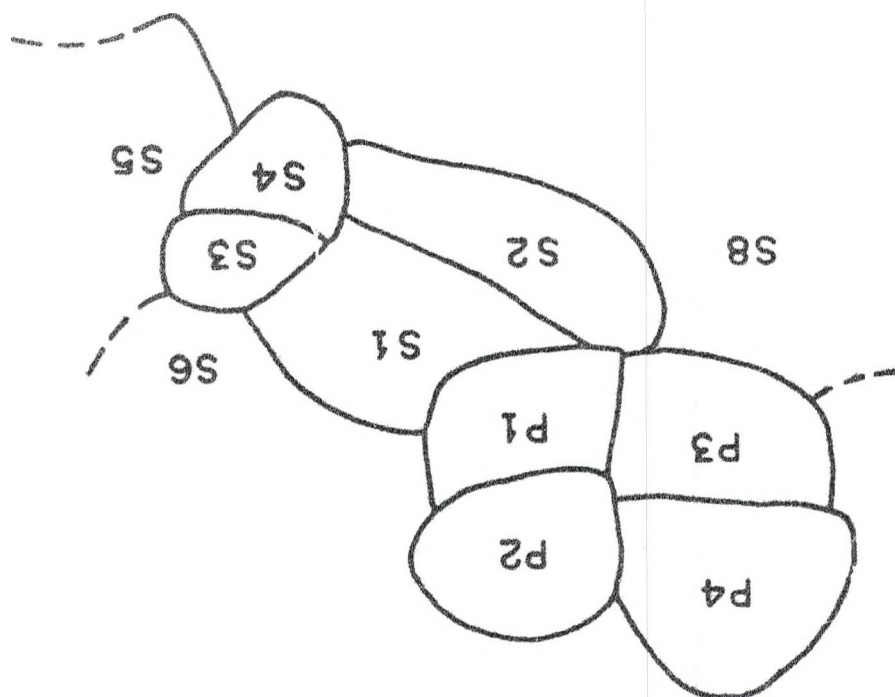


Figure 12. Territorial positions of sharptails (S) and prairie chickens (P) on the NeMar mixed ground, 24 April 1976.



10m

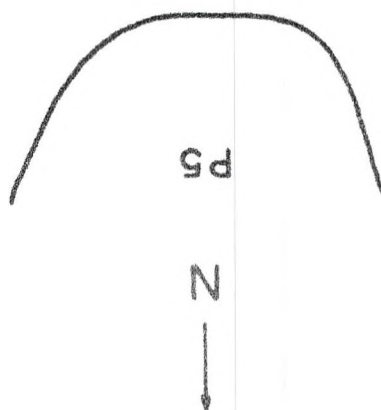


Figure 13. Territorial positions of prairie chickens (PC), sharptails (ST) and hybrids (F) on the ETymp display ground, 14 April 1978.

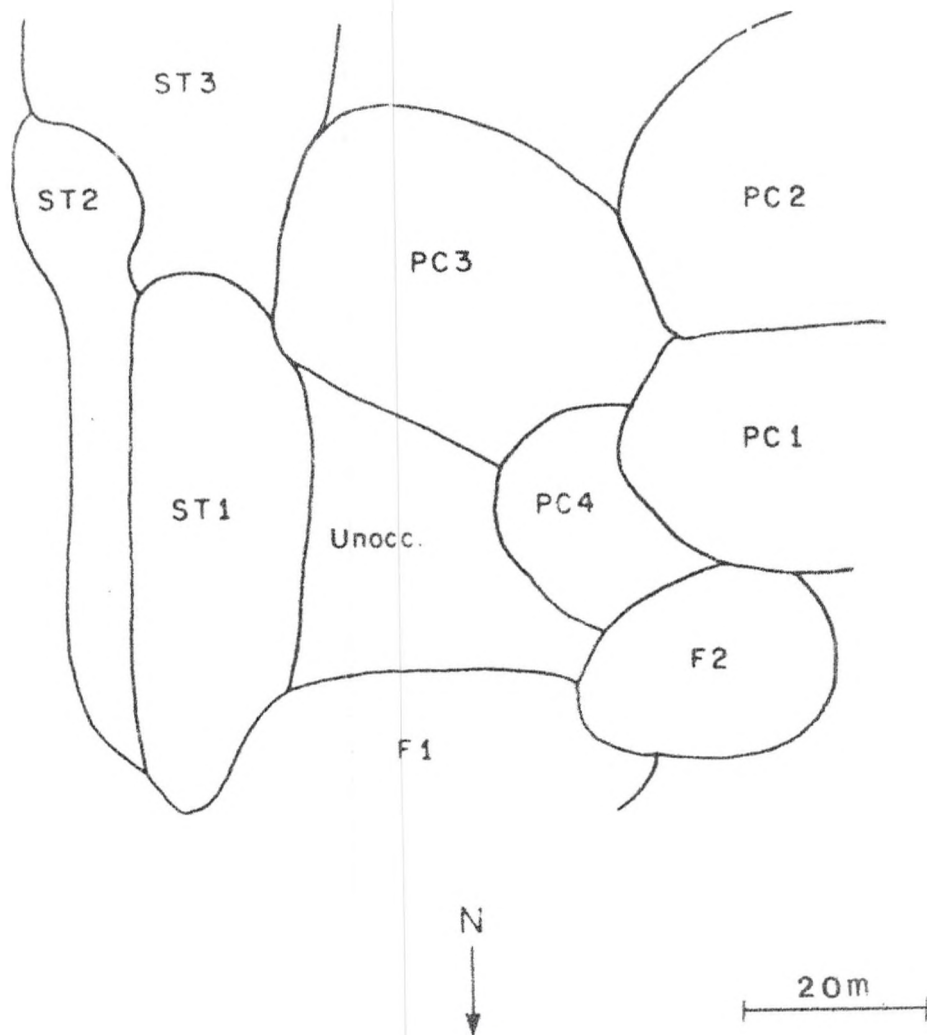
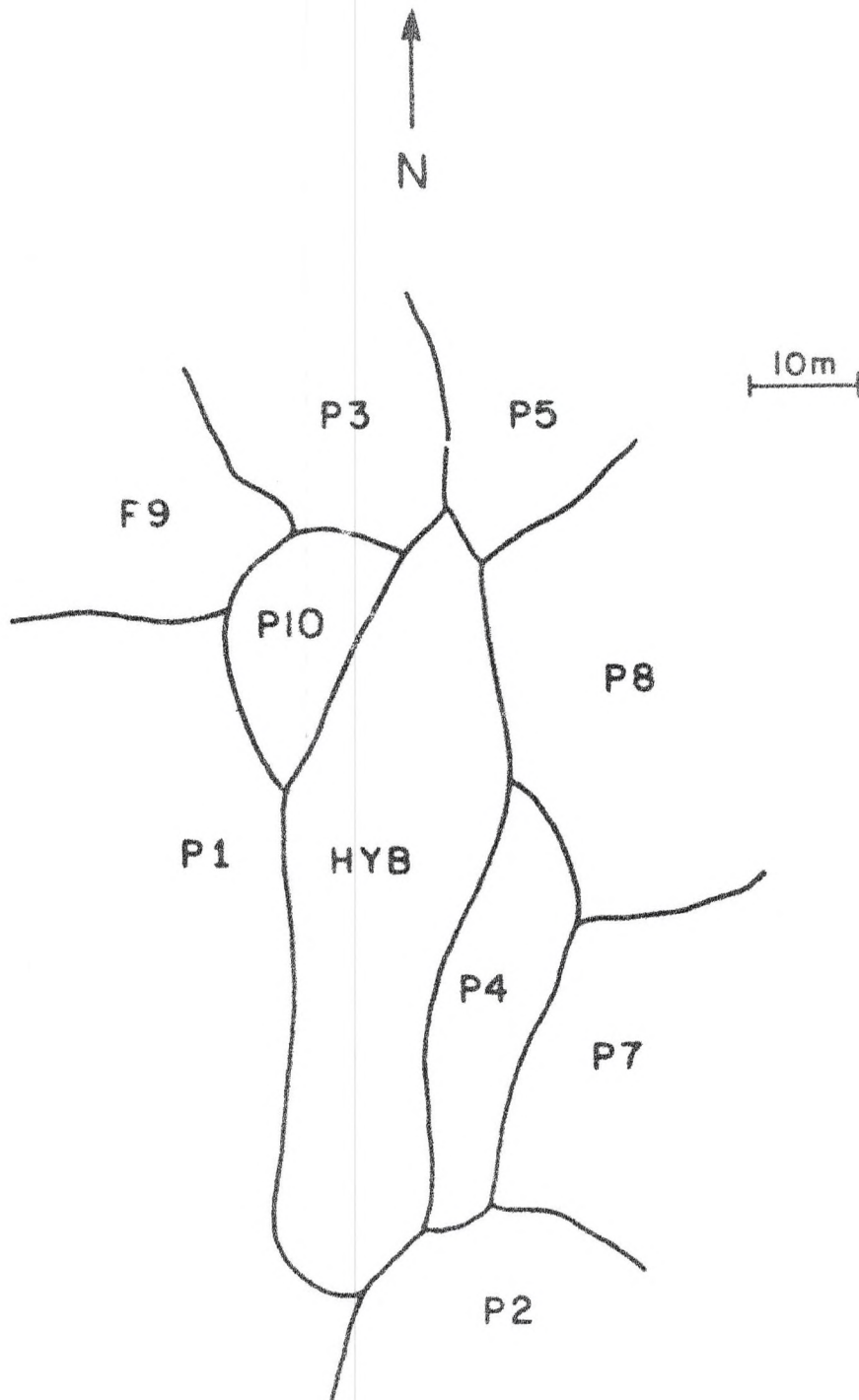


Figure 14. Territorial positions of prairie chickens (P) and hybrid (HYB) on the Pankratz booming ground, 22 April 1976.



stood with stretched necks and raised crests in 'upright alert' (Hjorth, 1970) while less-frightened birds simply raised their heads in "semi-alert" and did not differ between species.

Detailed Contrasts of Homologous Vocalizations

Four sets of vocalizations: coos and booms; chilks and whoops; whines; and cackles and their hybrid counterparts were obviously homologous and could be especially important in interspecific communication. Although booms, cooms and coos were sufficiently different to prevent confusion, calls in the other sets were less distinguishable and merit further attention. Discriminant analysis and canonical correlation were particularly useful in these contrasts.

Contrasts of whoops and chilks

Stepwise discriminant analysis identified all 8 characteristics listed in Table 5 as significant in distinguishing groups (= call x species combinations) with note duration and frequency measurements most important (Table 12). Four canonical variates were significant and the first 2 accounted for 91% of the variance. These had canonical correlations of 0.86 and 0.68, respectively.

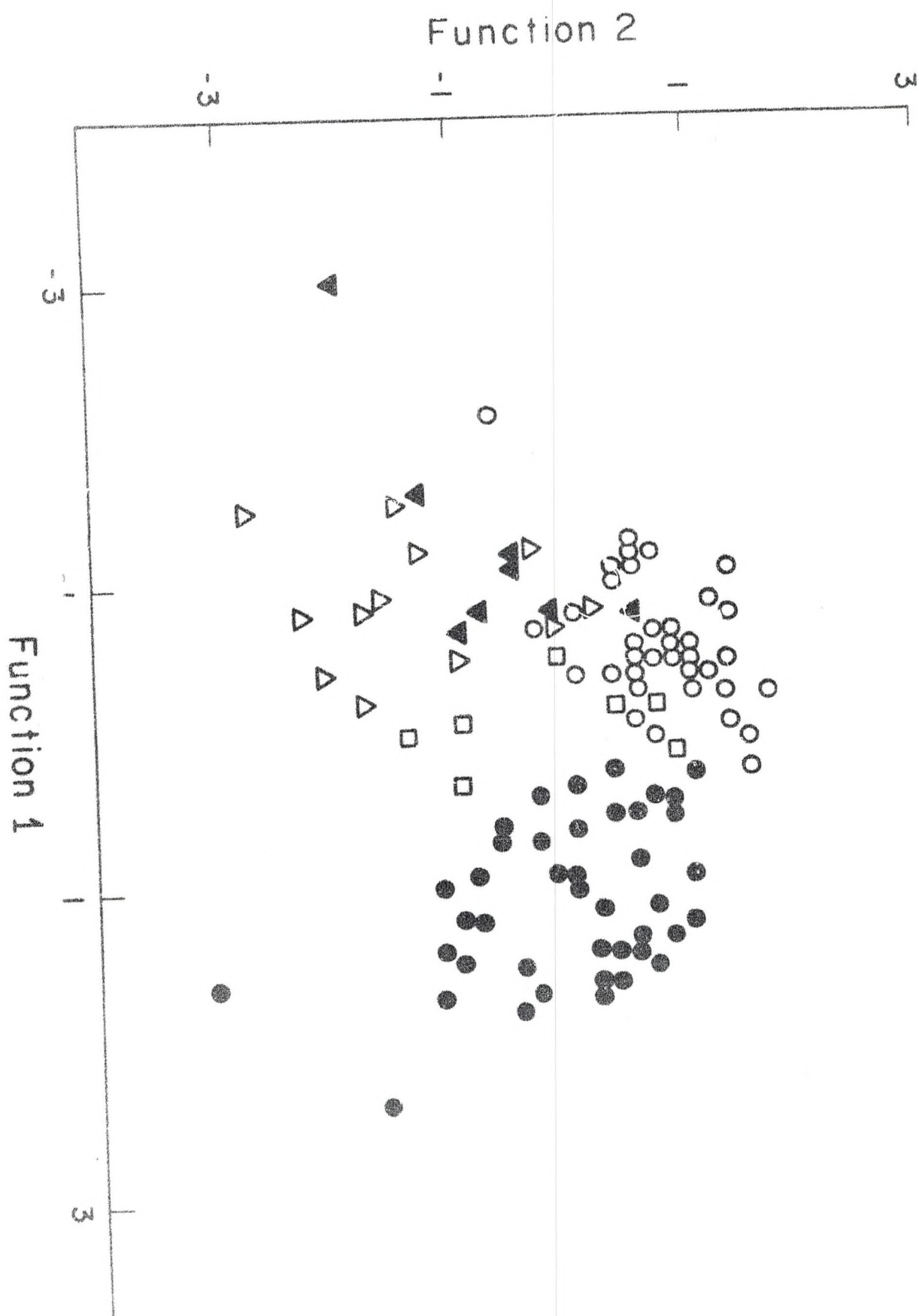
A plot of discriminant scores against the first 2 variates (Fig. 15) revealed that prairie chicken whoops and sharptail chilks could be readily discriminated along the first coordinate. The chilks of the WTymp hybrid were intermediate between those of both parental species and Pankratz hybrid whoops could be distinguished from sharptail and WTymp hybrid chilks along this axis. The second axis discriminated whoops of prairie chickens from those of the WTymp hybrid but not from

TABLE 12
RESULTS OF STEPWISE BACKWARDS DISCRIMINANT
ANALYSIS ON WHOOPS AND CHILKS

Step	Variable Entered	F to Enter	Wilk's Lambda	Rau's V	Significance
1	Note Duration	56.819	0.320	227.253	0.000
2	Strongest Frequency	20.412	0.181	380.574	0.000
3	Highest Frequency	7.071	0.142	416.718	0.000
4	Lowest Frequency	7.628	0.110	458.276	0.000
5	Frequency Modulation	3.270	0.098	476.155	0.001
6	Internote Interval	2.179	0.090	491.793	0.004
7	Number of Notes	2.701	0.081	512.886	0.000
8	Total Duration	1.120	0.078	528.932	0.003

Figure 15. Plot of prairie grouse whoops and chilks against the first two canonical variates.

Key: Empty circles = prairie chicken whoops
Filled circles = sharptail chilks
Filled triangles = Pankratz hybrid whoops
Empty triangles = WTymp hybrid whoops
Empty squares = WTymp hybrid chilks.



those of the Pankratz hybrid.

Strongest frequency loaded heaviest on variate 1, suggesting that the first axis was a reflection of frequency with lower frequencies to the left. Similarly, the second axis was related to note duration. The third and fourth axes helped distinguish other groups for an overall classification success of 84.8% (Table 13). Sharptail whines were the most unique call with a high percentage of correctly classified calls and no other vocalizations misclassified in this group. WTymp hybrid whoops had the highest percentage of misclassifications with some calls identified as Pankratz hybrid or prairie chicken whoops.

Contrasts of whines

Stepwise discriminant analysis of whines (Table 14) indicated that highest frequency, note duration and number of notes were most useful in discrimination. Two significant variates were extracted and accounted for 97.9% of the variance. They had correlations of 0.81 and 0.45, respectively.

Prairie chicken and sharptail whines were distinguished primarily along the first axis which was largely composed of highest frequency (Fig. 16). While the vocalizations of the Pankratz hybrid could be distinguished from those of sharptails and from the WTymp hybrid along this axis, they could not be separated from those of prairie chickens. Both coordinates were required to separate sharptail from WTymp hybrid whines. The second axis had number of notes as its major constituent.

TABLE 13

SUMMARY OF DISCRIMINANT ANALYSIS CLASSIFICATION
ON WHOOPS AND CHILKS

Actual Group	Classified Group					
	No. of Cases	WTymp Hybrid Whoops	WTymp Hybrid Chilks	Pankratz Hybrid Whoops	Prairie Chicken Whoops	Sharptail Chilks
WTymp Hybrid Whoops	12	7 58.3%	0	3 25.0%	2 16.7%	0
WTymp Hybrid Chilks	8	0	6 75.0%	0	2 25.0%	0
Pankratz Hybrid Whoops	8	0	0	7 87.5%	1 12.5%	0
Prairie Chicken Whoops	41	0	2 4.9%	2 4.9%	37 90.2%	0
Sharptail Chilks	43	0	4 9.3%	0	1 2.3%	38 88.4%

TABLE 14

SUMMARY OF STEPWISE DISCRIMINANT ANALYSIS
ON PRAIRIE GROUSE WHINES

Step	Variable Entered	F	Rao's V	Significance
1	Highest Frequency	44.67	134.00	0.000
2	Note Duration	12.35	209.84	0.000
3	Number of Notes	8.25	235.89	0.000
4	Internote Interval	1.36	243.39	0.058

Figure 16. Plot of prairie grouse whines against first two canonical variates.

Key: Empty circles = prairie chickens
Filled circles = sharptails
Filled triangles = WTymp hybrid
Empty squares = Pankratz hybrid.

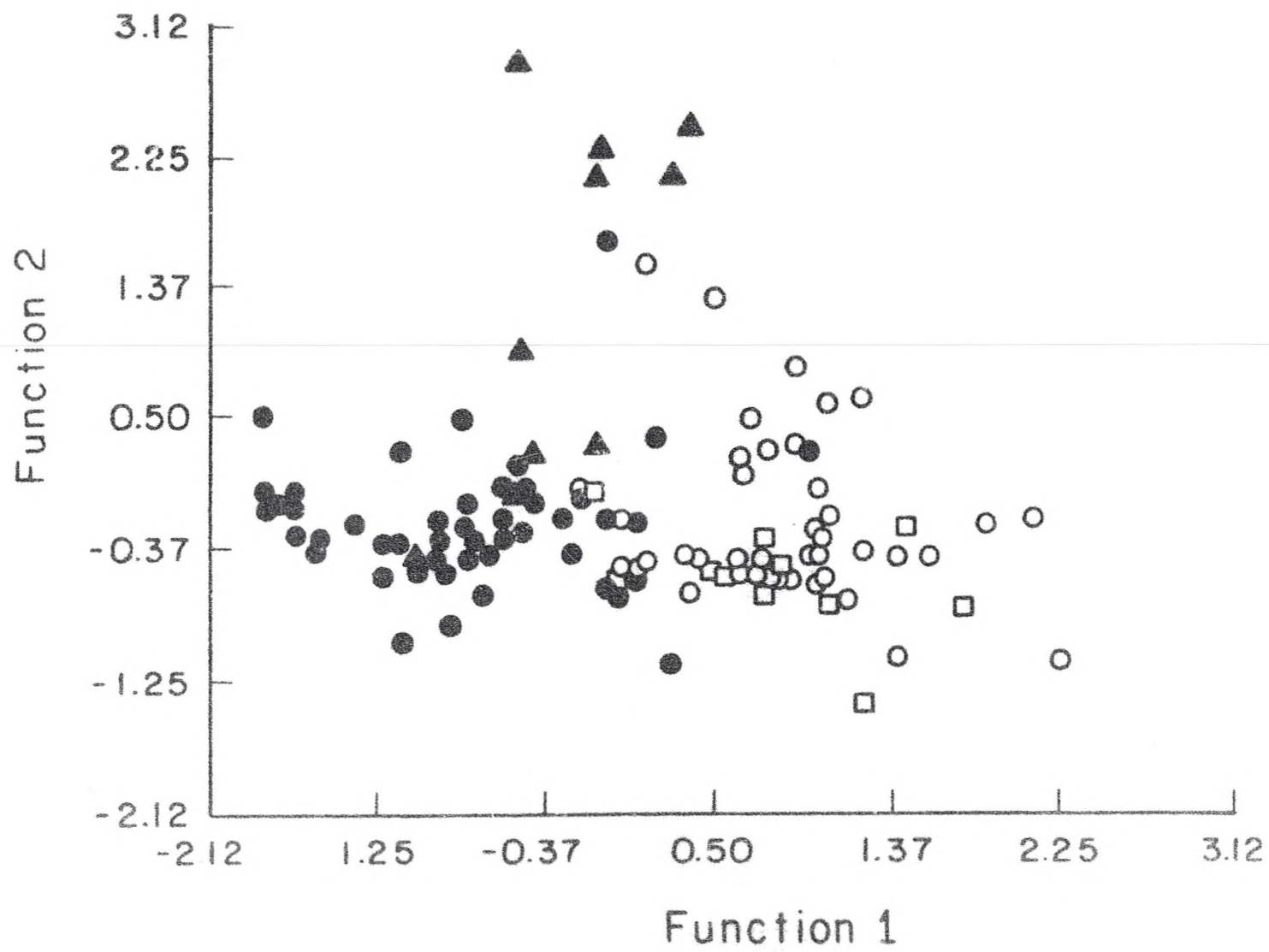


TABLE 15

SUMMARY OF DISCRIMINANT ANALYSIS CLASSIFICATION
ON PRAIRIE GROUSE WHINES

Actual Group	No. of Cases	Classified Group			
		Prairie Chicken	Sharptail	Pankratz Hybrid	WTymp Hybrid
Prairie Chicken	42	27 64.3%	2 4.8%	10 23.8%	3 7.1%
Sharptail	49	1 2.0%	42 85.7%	4 8.2%	2 4.1%
Pankratz Hybrid	11	3 27.3%	1 9.1%	7 63.6%	0
WTymp Hybrid	10	0	3 30.0%	0	7 70.0%

Overall success of classification was 74.1% (Table 15). Many of the whines from prairie chickens were misclassified as those of the Pankratz hybrid. This hybrid's whines, however, were more correctly classified, undoubtedly because of the smaller sample size. Fourteen percent of the sharptail whines were in wrong groups with the majority of these sorted into the Pankratz hybrid's category. Only 3 of 91 (3.3%) parental whines were in heterospecific groups.

Contrasts of Cackles

The stepwise analysis of cackles revealed that 9 characteristics were significant in distinguishing groups (Table 16). Of these, temporal characteristics were most important. Two canonical variates were significant, accounted for 96.5% of the variance and had correlations of 0.78 and 0.68, respectively. These variates clearly distinguished WTymp hybrid cackles along the first coordinate and sharptail cackles along the second (Fig. 17). Cackles from prairie chickens and the Pankratz hybrid could not be distinguished. In this analysis, the first variate was composed primarily of lowest and strongest frequencies while the second had temporal characteristics as its major constituents.

Cackles were classified with 76.8% success (Table 17). All cackles from the WTymp and Pankratz hybrids were correctly classified, partly because of small sample sizes. Perhaps more importantly, over 10 prairie chicken cackles were identified as those of the Pankratz hybrid's but only 1 call was placed in the WTymp hybrid's group. Ten of 101 (9.9%) parental species' cackles were placed in heterospecific groups.

TABLE 16
SUMMARY OF STEPWISE DISCRIMINANT ANALYSIS
ON PRAIRIE GROUSE CACKLES

Step	Variable Entered	F	Rao's V	Significance
1	Number of Notes	13.63	40.88	0.000
2	Note Duration	1.95	48.72	0.049
3	Total Duration	13.20	91.04	0.000
4	Internote Interval	9.62	127.24	0.000
5	Frequency Modulation	4.91	150.59	0.000
6	Number of Freq. Bands	5.78	182.36	0.000
7	Low Frequency	2.42	197.22	0.002
8	Strong Frequency	5.06	232.20	0.000
9	High Frequency	5.83	261.34	0.000

Figure 17. Plot of prairie grouse cackles against first two canonical variates.

Key: Empty circles = prairie chickens
Filled circles = sharptails
Empty squares = Pankratz hybrid
Filled triangles = WTymp hybrid.

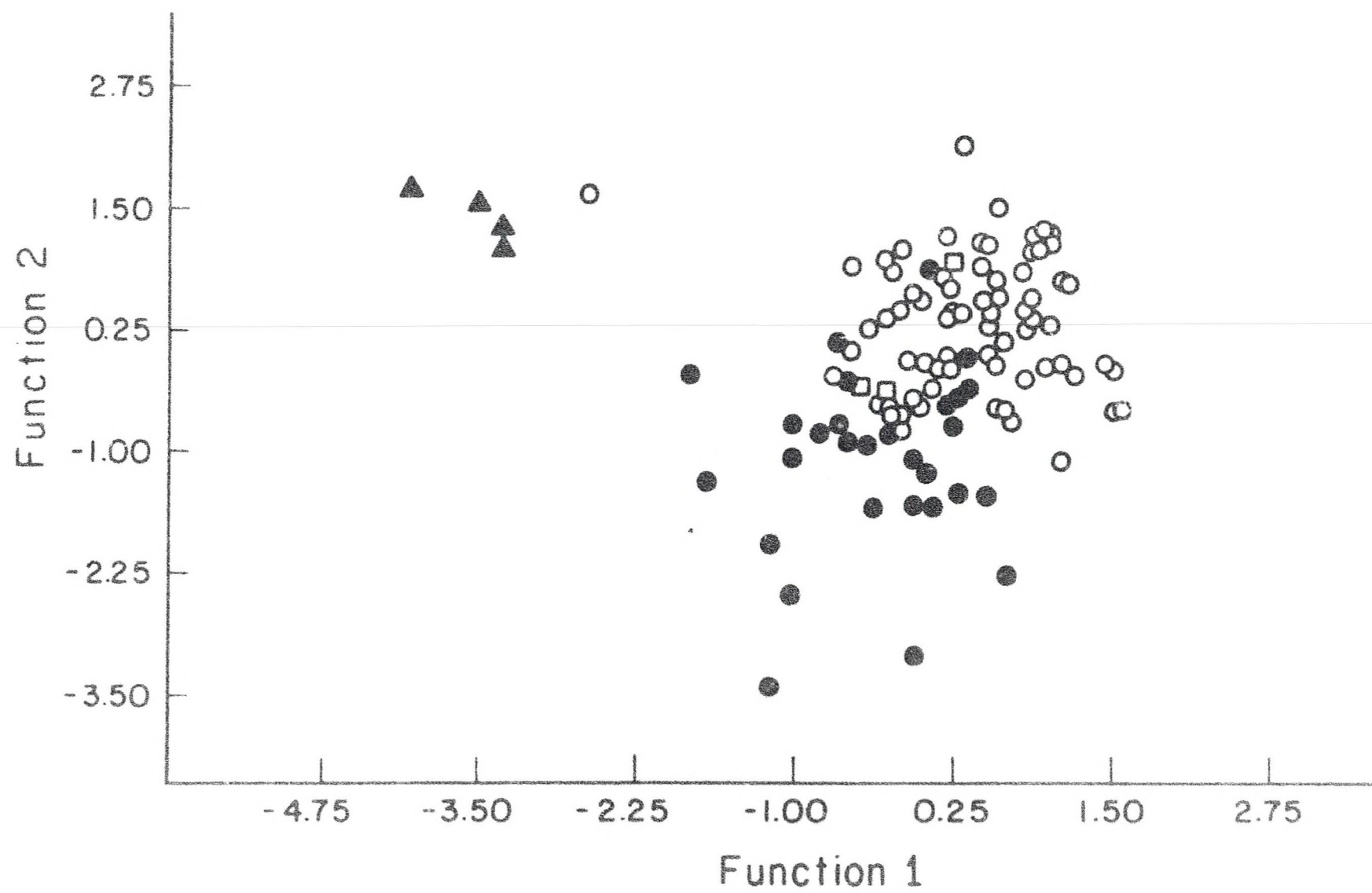


TABLE 17

SUMMARY OF DISCRIMINANT ANALYSIS CLASSIFICATION
ON PRAIRIE GROUSE CACKLES

Actual Group	No. of Cases	Classified Group			
		Prairie Chicken	Sharptail	Pankratz Hybrid	WTymp Hybrid
Prairie Chicken	72	51 70.8%	7 9.7%	13 18.1%	1 1.4%
Sharptail	29	3 10.3%	25 86.2%	1 3.4%	0
Pankratz hybrid	4	0	0	4 100.0%	0
WTymp Hybrid	4	0	0	0	4 100.0%

Temporal Occurrence of Displays

This section examines the frequency of occurrence of common male displays in relation to daily and seasonal time periods. Based on arrival times of males, daily periods were divided into early (arrival to a half hour after arrival), mid (early to a half hour before departure) and late (mid until departure) morning. Weekly rates of activity were compared to periods of hen visitations: weeks 1-4 were characterized by few female visitations; 5-11 included peaks of hen visitations; and 12-13 had no hens.

Daily patterns of male displays

Prairie chickens

The most common prairie chicken behaviors were booms, stamps, whoops, whines and cackles. Of these, whines were most frequent throughout the morning (Table 18) and only comfort movements increased in late morning.

Sharptails

Sharptails appeared to be more active than prairie chickens through the entire morning (Table 19). Several behaviors including whines, coos, walk, comfort and gobbles were frequent throughout the periods but dancing, chilks and cork notes were common only in early morning.

Hybrid

The major activities of the Pankratz hybrid included whines, cooms, whoops, stamps and gobbles (Table 20). Almost all behaviors except gobbles and comfort movements ceased by late morning.

TABLE 18

RATES OF COMMON PRAIRIE CHICKEN BEHAVIORS WHEN
HENS ARE PRESENT AND THROUGH MORNINGS

		Acts Per Minute									
Context		Face Off	Forward Rush	Boom	Stamp	Whoop	Whine	Cackle	Flutter Jump	Fight	Comfort
Hen Present ^a (N = 21) ^b	\bar{X}	0.19	0.69	11.83	11.29	5.96	8.83	2.06	1.02	1.54	0.00
	SE	0.06	0.16	0.88	1.25	1.75	2.13	0.61	0.32	0.95	0.00
Early Morning (N = 18)	\bar{X}	0.18	0.18	8.21	5.84	1.44	14.57	2.56	0.85	0.07	0.22
	SE	0.07	0.07	0.88	0.97	0.49	2.60	0.47	0.24	0.04	0.11
Mid Morning (N = 102)	\bar{X}	0.25	0.22	2.69	1.07	0.32	9.11	1.03	0.11	0.10	1.13
	SE	0.04	0.41	0.31	0.22	0.09	1.23	0.21	0.04	0.03	0.11
Late Morning (N = 35)	\bar{X}	0.11	0.03	0.91	0.33	0.04	2.44	0.36	0.01	0.01	1.53
	SE	0.05	0.02	0.30	0.17	0.03	1.00	0.16	0.01	0.01	0.18

^aConspecific hens only.

^bSample sizes refer to number of samples taken.

TABLE 19

RATES OF COMMON SHARPTAIL BEHAVIORS WHEN HENS
ARE PRESENT AND THROUGH MORNINGS

		Acts Per Minute										
Context		Gobbles	Face Off	Forward Rush	Coo	Dancing	Chilk	Cork Notes	Whines	Cackles	Fight	Comfort
Hen Present ^a (N = 24) ^b	\bar{X}	1.43	1.05	0.29	1.78	4.33	13.52	9.29	1.30	0.43	0.19	0.24
	SE	0.68	0.17	0.09	0.79	0.53	2.59	1.46	0.43	0.14	0.11	0.09
Early Morning (N = 25)	\bar{X}	3.98	0.46	0.21	3.74	1.18	1.19	1.20	0.89	0.01	0.21	2.30
	SE	0.98	0.12	0.07	1.04	0.51	0.44	0.67	0.50	0.01	0.09	0.77
Mid Morning (N = 90)	\bar{X}	1.38	0.59	0.15	2.62	0.21	0.23	0.37	0.68	0.11	0.07	2.90
	SE	0.27	0.08	0.04	0.49	0.06	0.10	0.16	0.22	0.04	0.03	0.50
Late Morning (N = 44)	\bar{X}	1.67	0.58	0.05	1.21	0.10	0.04	0.00	0.66	0.06	0.06	3.72
	SE	0.52	0.12	0.03	0.36	0.05	0.04	0.00	0.35	0.03	0.03	1.00

^aConspecific hens only.

^bSample sizes refer to number of samples taken.

TABLE 20

RATES OF COMMON BEHAVIORS OF THE PANKRATZ HYBRID
WHEN HENS ARE PRESENT AND THROUGH MORNINGS

		Acts Per Minute									
Context		Face Off	Forward Rush	Coom	Stamp	Whoop	Whine	Cackle	Fight	Comfort	Gobble
Hen Present ^{a,b} (N = 8)	\bar{X}	0.83	1.74	7.72	6.45	7.69	6.54	1.29	0.04	0.42	0.00
	SE	0.50	0.55	2.89	2.70	4.03	3.51	0.69	0.06	0.46	0.00
Early Morning (N = 3)	\bar{X}	0.87	1.22	3.33	3.22	2.11	15.11	0.33	0.33	0.89	0.00
	SE	0.44	0.62	2.40	2.59	1.10	8.58	0.33	0.19	0.89	0.00
Mid Morning (N = 17)	\bar{X}	0.79	0.71	1.32	0.57	0.78	9.07	0.28	0.35	0.79	1.01
	SE	0.22	0.19	0.64	0.24	0.28	2.27	0.09	0.10	0.25	0.35
Late Morning (N = 5)	\bar{X}	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.89	0.33
	SE	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.57	0.33

^aPrairie chicken hen only.

^bSample sizes refer to number of samples taken.

Seasonal patterns of behaviors

Prairie chickens

As with morning activities, the most common prairie chicken behaviors throughout the season were booms and whines (Fig. 18). Several behaviors showed seasonal perturbations. Face offs and fighting, for example, were highest in early spring but gradually diminished as territories stabilized and other behaviors took precedence. Whoops, stamps, booms and flutter jumps peaked during major hen visitation periods.

Sharptails

Sharptails maintained higher activity levels through the season than did prairie chickens (Fig. 19). Perturbations also occurred in most behaviors with chilks, flutter jumps, whines and dances peaking during major hen visitation periods. Gobbles and face offs were common in early season but, while gobbles steadily declined, face offs increased during weeks 4-5 and 9. These weeks corresponded to increases in most behaviors. Coos were initially low but increased rapidly in the third week and remained high through most of the remaining spring.

Hybrid

There were insufficient samples to examine hybrid behaviors on a weekly basis, but 5-week divisions showed that whines were most common throughout the spring (Table 21). Cooms, whoops, stamps and gobbles increased from early to late spring while other behaviors remained constant but infrequent.

Figure 18. Frequency of occurrence of common prairie chicken behaviors through the 1976 breeding season. Week 1 begins 1 March and the sampling period extends through May. Vertical axis is number of acts per minute and N is number of samples for a particular week.

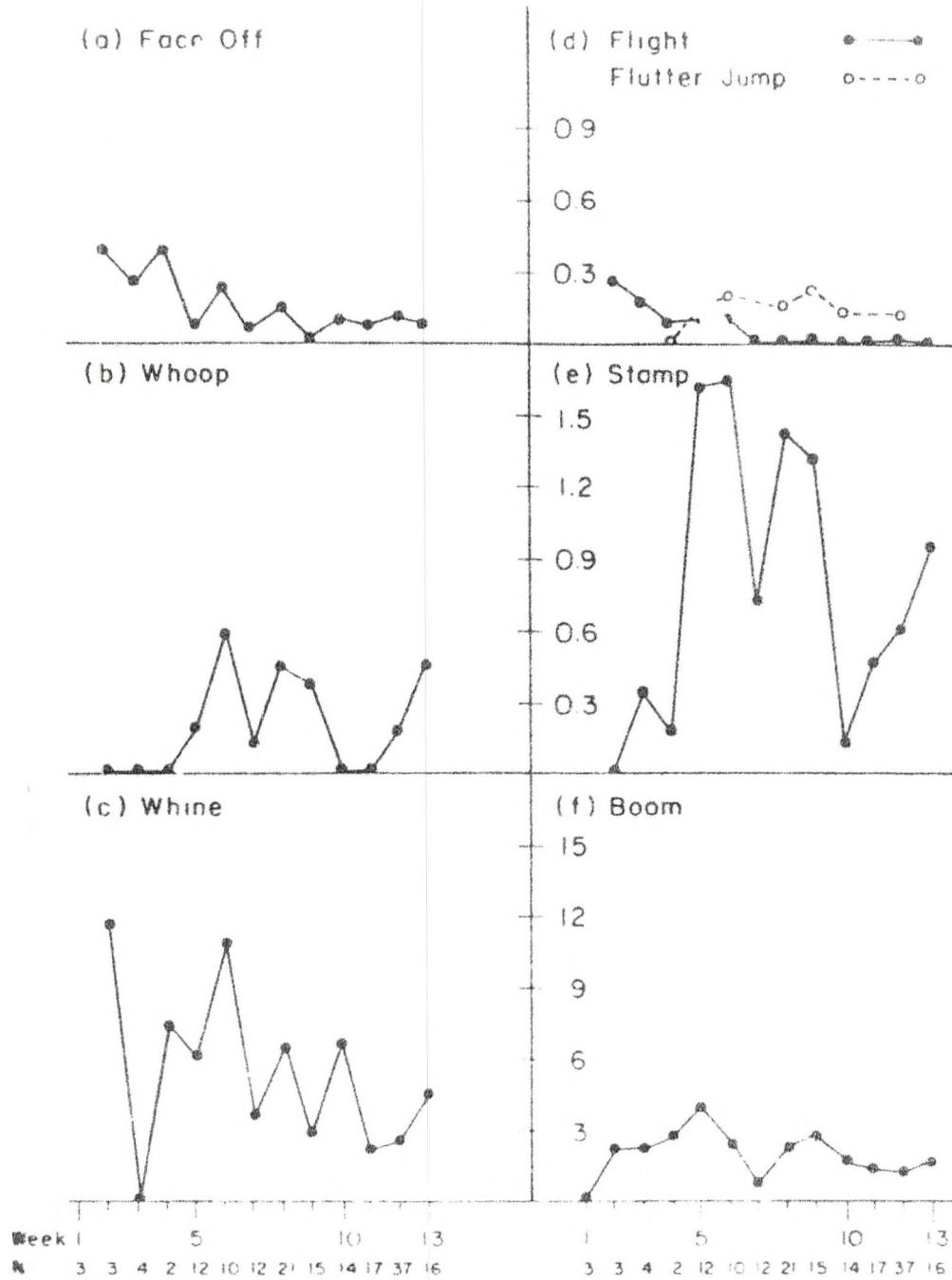


Figure 19. Frequency of occurrence of common sharptail behaviors during the 1976 breeding season. Week 1 began 1 March and the sampling period extends through May. Vertical axis is in number of acts per minute and N is number of samples per week.

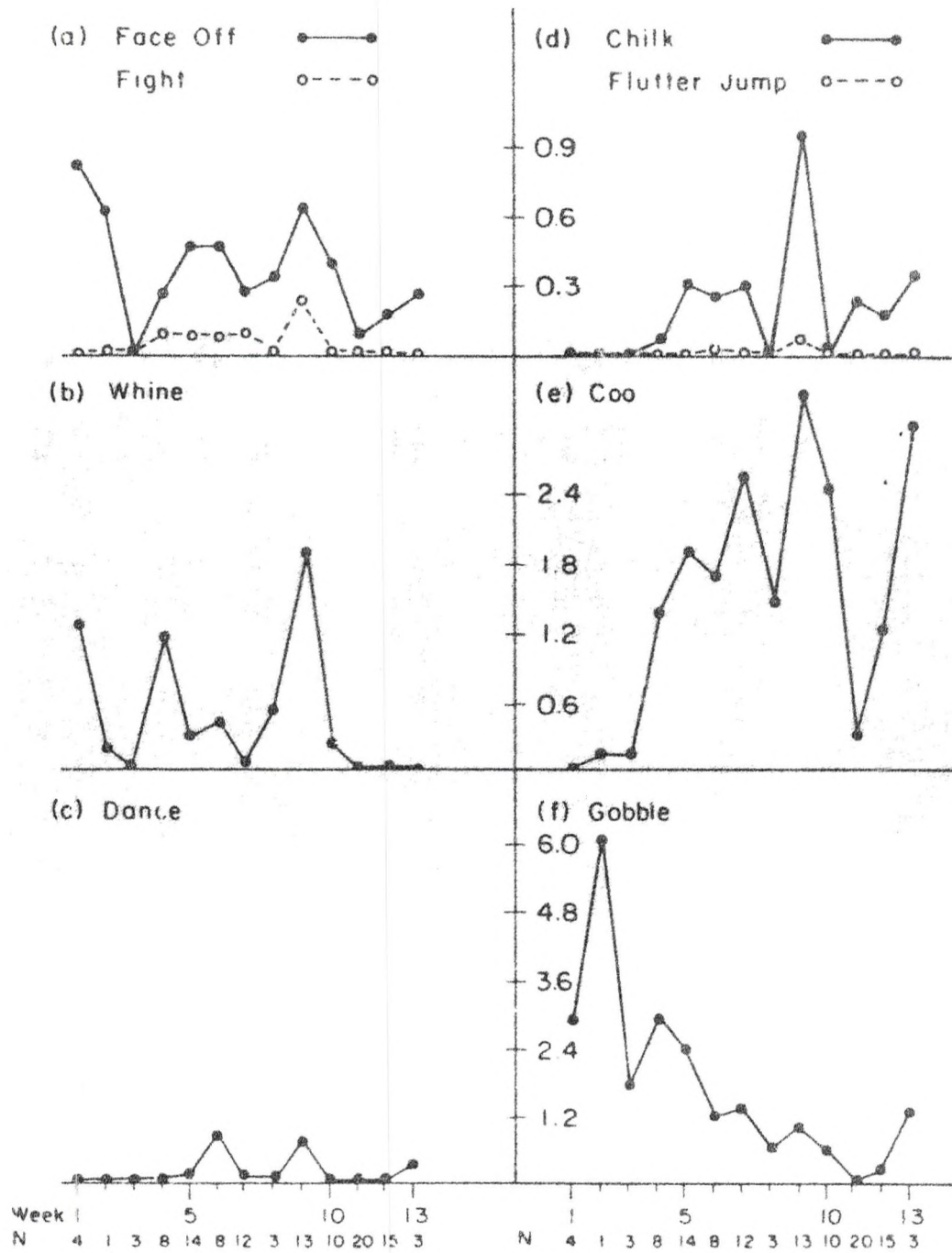


TABLE 21
RATES OF COMMON BEHAVIORS OF THE PANKRATZ HYBRID
THROUGH THE SPRING BREEDING SEASON OF 1976

		Acts Per Minute									
Period ^a		Face Off	Forward Rush	Coom	Stamp	Whoop	Whine	Cackle	Fight	Comfort	Gobble
Pre-peak ^b (N = 3)	\bar{X}	1.56	0.33	0.00	0.11	0.00	6.73	0.33	0.44	0.00	1.00
	SD	1.39	0.58	0.00	0.19	0.00	5.94	0.33	0.77	0.00	0.67
Peak (N = 4)	\bar{X}	1.50	1.00	1.58	1.50	2.17	16.08	0.33	0.50	0.00	0.00
	SD	0.33	0.55	1.17	1.50	0.43	8.35	0.47	0.33	0.00	0.00
Post-peak (N = 6)	\bar{X}	0.61	1.37	3.92	2.11	1.83	12.26	0.39	0.44	0.44	1.59
	SD	0.74	0.92	4.38	3.16	1.62	11.07	0.39	0.40	1.09	1.75

^aPeriod refers to peaks in hen visitations.

^bSample size refers to number of samples taken.

Relationships Among Prairie Grouse Displays

Relationships among prairie chicken displays

Transitions

Appendix II shows that only whines, booms and whoops were highly repetitive. Whines and cackles were very likely to follow each other as were stamps and booms. Cackles also frequently followed flutter jumps which, in turn, came after booms. Walk and alert tended to follow comfort movements.

Correlation clusters

Prairie chicken behaviors could be divided into 3 main clusters based on the correlation dendrogram (Fig. 20, correlation matrix in Appendix III). The top cluster, face off to cackle, included close-contact, agonistic behaviors. Cackles clustered to this group at a low cophenetic value and were only loosely associated with it. The second cluster (forward to run parallel) included some behaviors (stamp, whoop and flutter jump) which were usually involved in courtship and others (forward, forward rush and run parallel) involved in agonistic contexts. The last cluster (walking to comfort) was made up of low-priority behaviors that were not highly correlated with other activities. Whines and booms, which did not join any cluster, occurred in many situations and were not highly associated with any particular activity.

Distance clusters

In the dendrogram based on distance values (Fig. 21, distance matrix in Appendix IV), the first 9 behaviors clustered very tightly

Figure 20. Cluster analysis of prairie chicken activities based on correlations. Cophenetic correlation = 0.86.

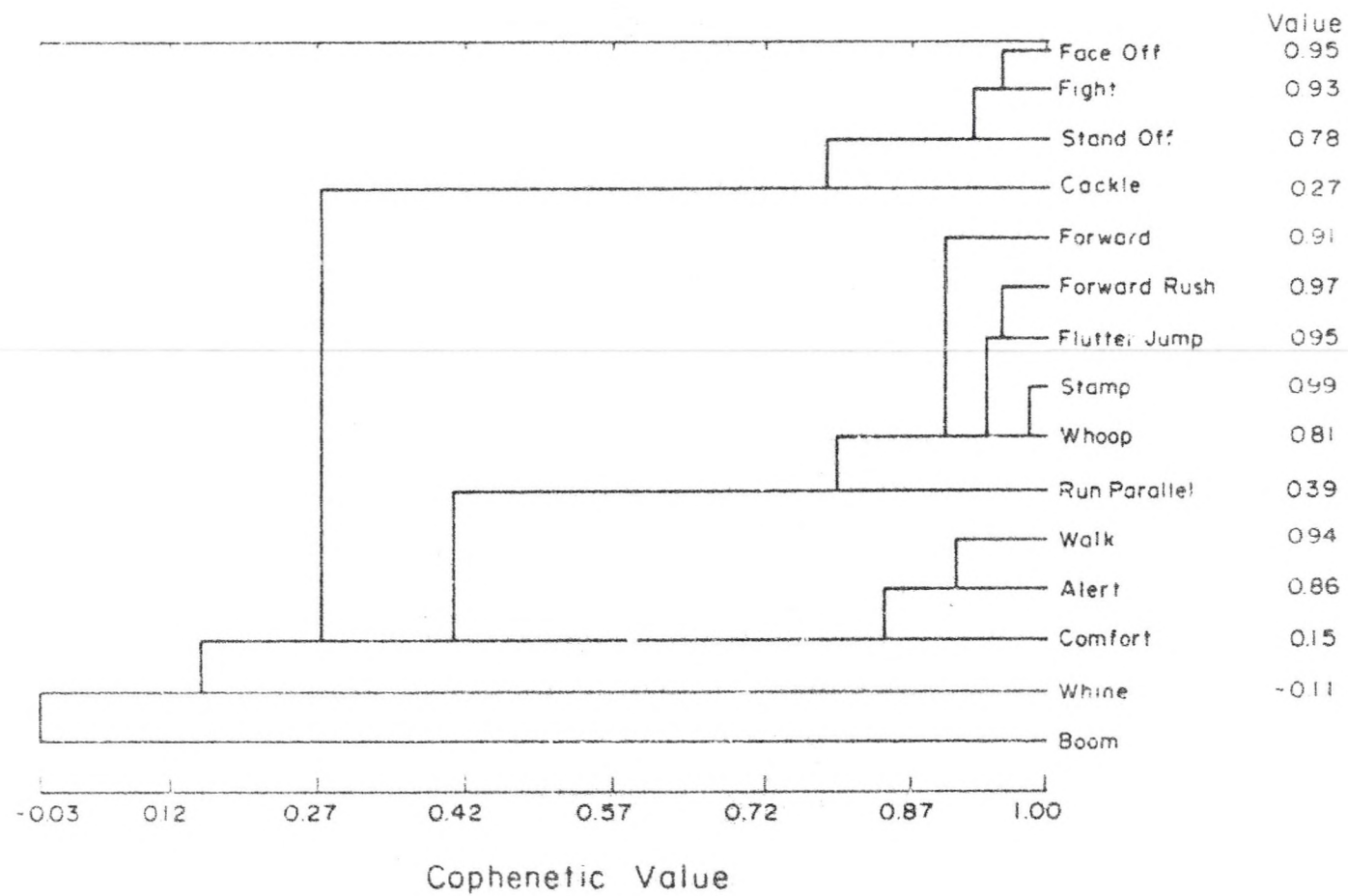
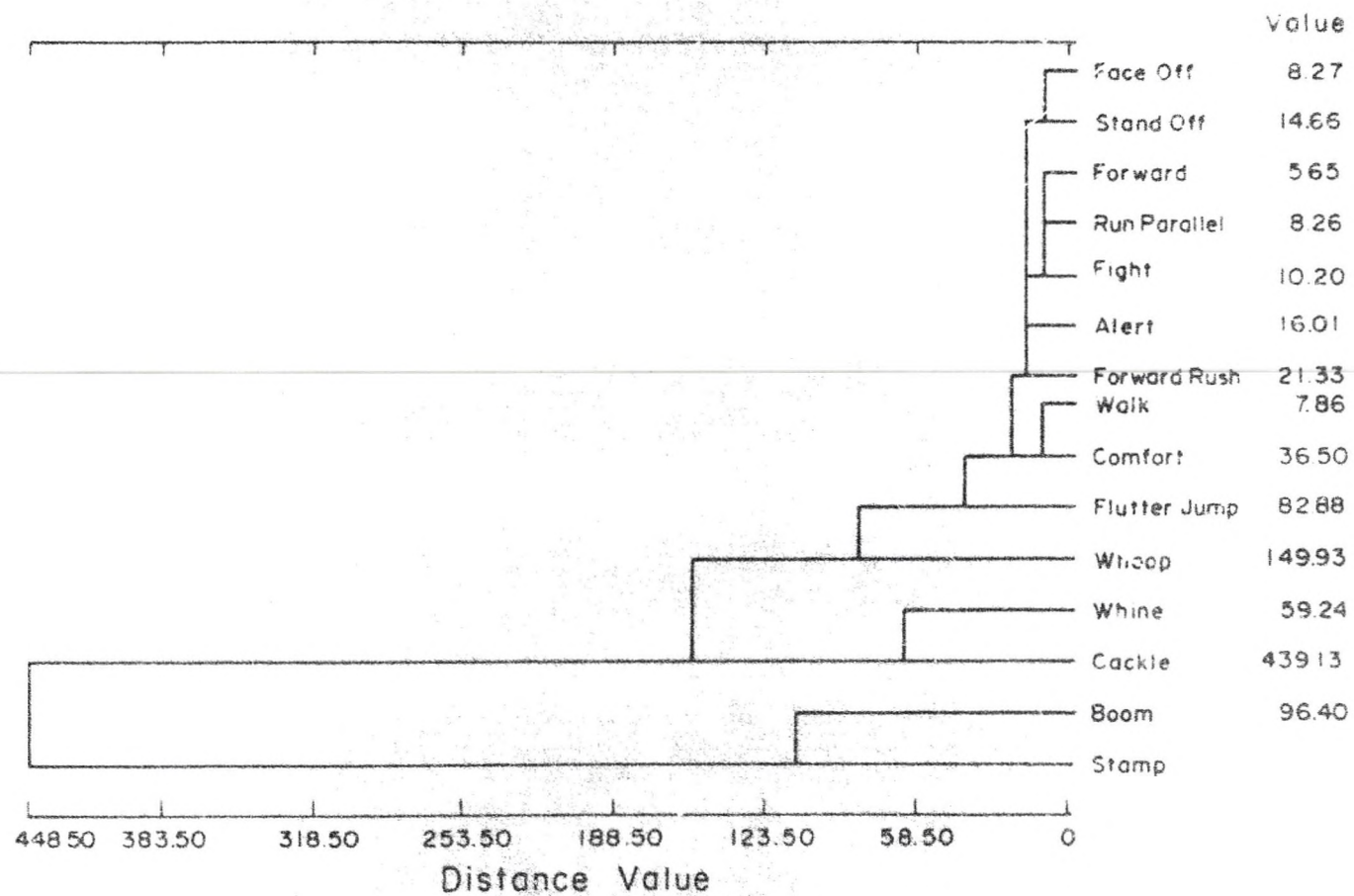


Figure 21. Cluster analysis of prairie chicken activities based on distance coefficients. Cophenetic correlation = 0.96.



and were involved in agonistic contexts or personal maintenance. The differences among these behaviors were so small that only agonistic and personal maintenance activities could be distinguished. Whines and cackles clustered as did booms and stamps, but whoops and flutter jumps did not clearly belong to any group. Cophenetic correlations indicated that both dendrograms were good representations of their respective matrices.

Relationships among sharptail displays

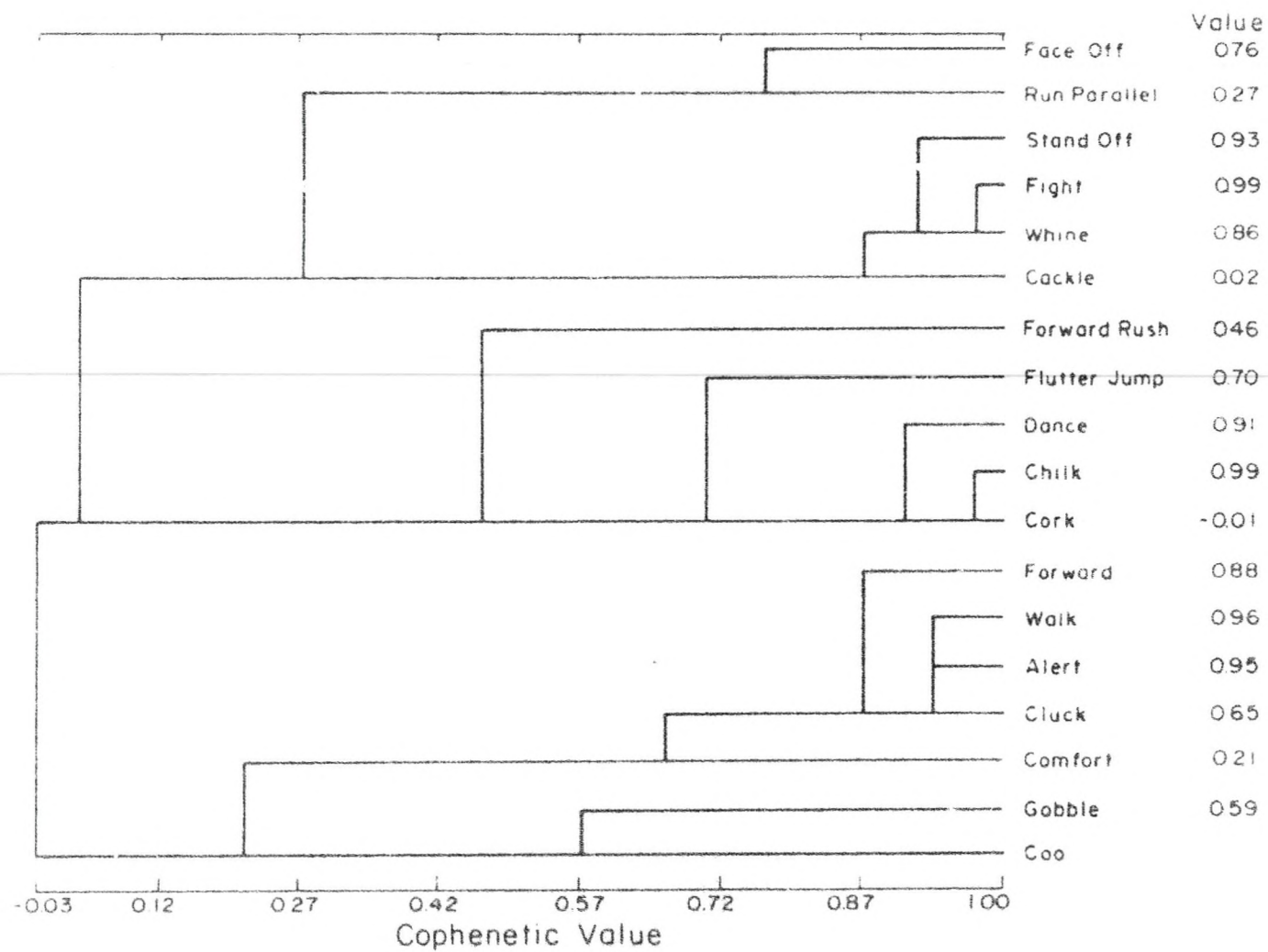
Transitions

Repetitions were very common in sharptail whines, chilks, cork notes, coos and gobbles; were only occasional in dances and comfort movements and rare or absent in other behaviors (Appendix II). Face offs were frequently followed by stand offs and fights. Cork notes and chilks were followed most often by dances. Coos and gobbles and cork notes and dances were also closely associated.

Correlation clusters

The dendrogram based on correlations (Fig. 22, correlation matrix in Appendix III) divided behaviors into 5 loose clusters. The first (face off and running parallel) and second (stand off to cackle) clusters were composed of agonistic activities. The third (forward rush to cork notes) contained behaviors found in courtship and the fourth (forward to comfort) was comprised of maintenance, non-communicatory or low-level alarm behaviors. Gobbles and coos formed a fifth group but were only loosely associated with each other or with other groups.

Figure 22. Cluster analysis of sharptail activities based on correlations. Cophenetic correlation = 0.87.



Distance clusters

This dendrogram (Fig. 23, distance matrix in Appendix IV) readily separated dances, chilks and cork notes from the major cluster of other activities. Small subgroups such as cluck and alert, fight and cackle and stand off and whine, which were useful in determining relationships of acoustical and visual displays, could be discerned in the major cluster.

Relationships among hybrid displays

Transitions

The only highly repetitive behaviors of the Pankratz hybrid were whines and whoops (Appendix II). Whines were frequently followed by cackles, face offs and fights; and, in turn, face offs and fights commonly preceded whines. Stamps, whoops and cooms were associated with each other as were flutter jumps and cackles.

Correlation clusters

The correlation dendrogram (Fig. 24, matrix in Appendix III) was composed of 5 clusters and an independent forward. The first (face off to fight) and second (cackle to gobble) clusters included many agonistic behaviors. Whines and flutter jumping; cooms, whoops and stamps; and comfort and walk formed the other groups.

Distance clusters

The dendrogram based on distance coefficients (Fig. 25, Appendix IV) consisted of 3 clusters. The first (face off to whine) was primarily agonistic, the second (forward rush to cackle) included a

Figure 23. Cluster analysis of sharptail activities based on distance coefficients. Cophenetic correlation = 0.94.

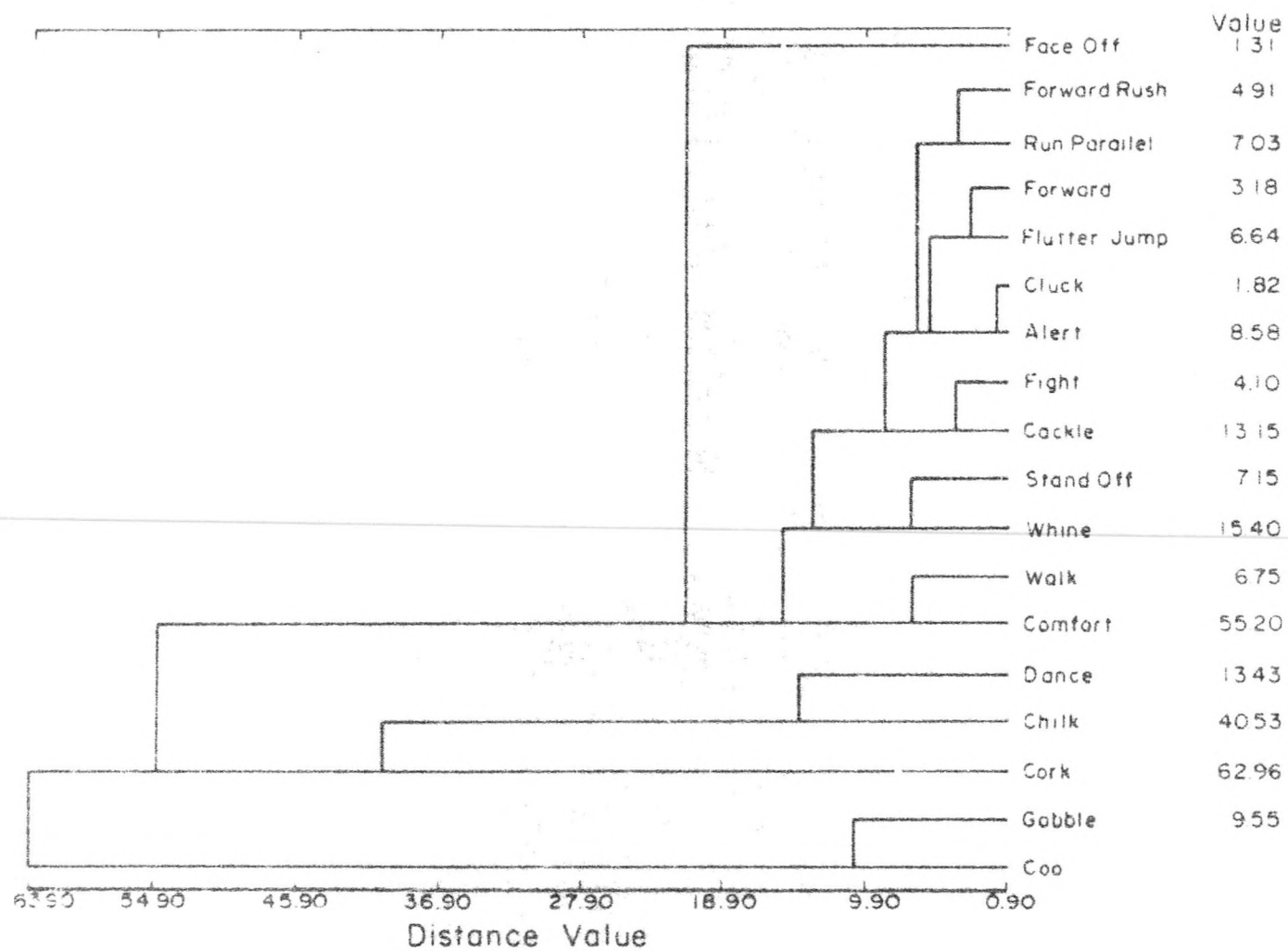


Figure 24. Cluster analysis of Pankratz hybrid activities based on correlations. Cophenetic correlation = 0.81.

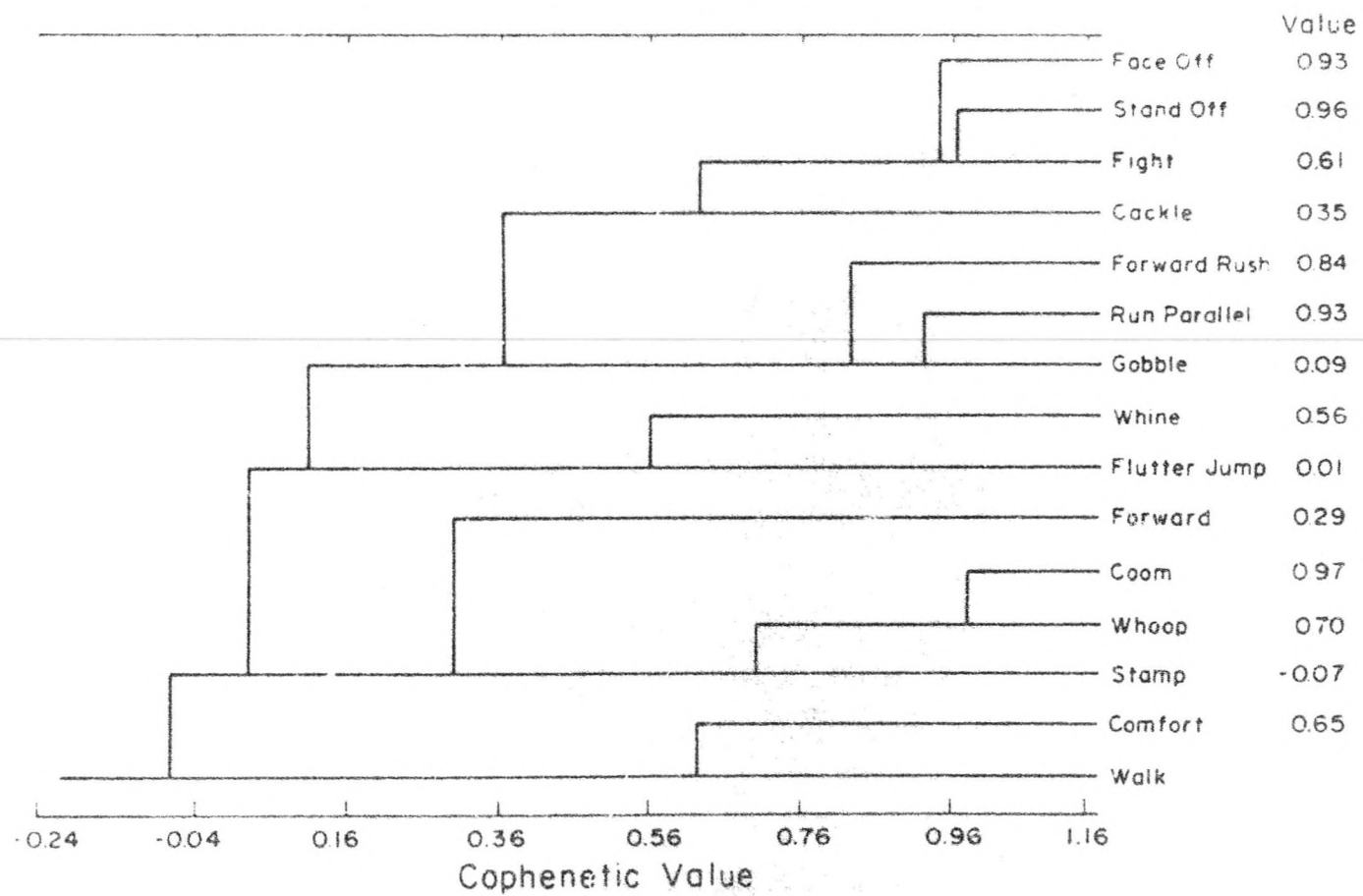
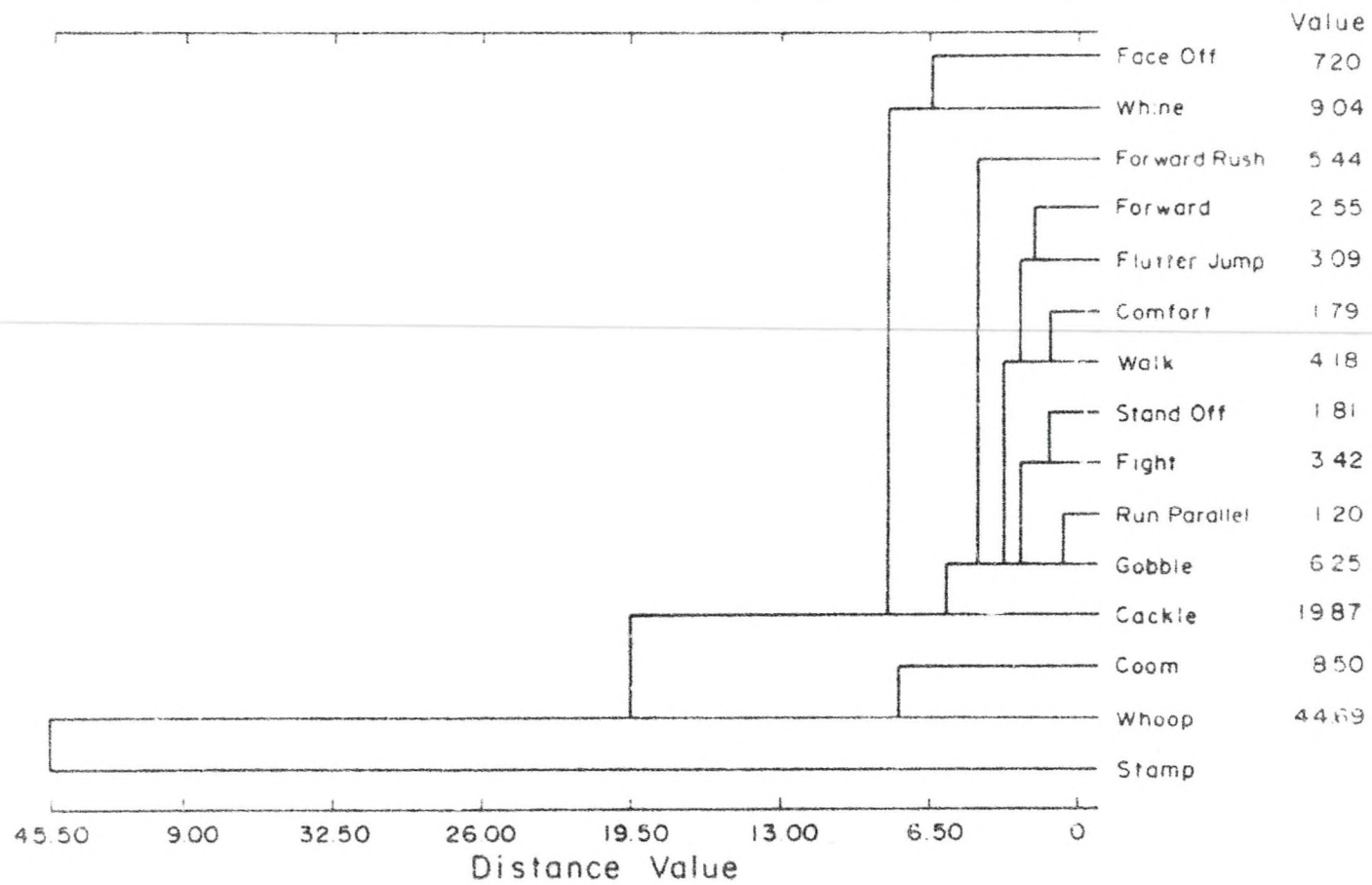


Figure 25. Cluster analysis of Pankratz hybrid activities based on distance coefficients. Cophenetic correlation = 0.96.



variety of behaviors involved in agonistic contexts and comfort movements and the third (coo to stamp) contained epigamic behaviors.

Discussion

Information Content and Functions of Prairie Grouse Displays

Although the function(s) of a display cannot be proven without experimentation, some estimate of the information present in a display can be determined by identifying the contexts in which it occurs. The following section discusses what information is present in common prairie grouse displays and speculates on their functions.

Prairie chicken displays

Booms and booming displays

Booms and associated visual displays occurred in a variety of contexts and were loosely associated with other behaviors. Thus, they probably are polyvalent and convey the following information:

1. identification of sex - only males boomed and booming displays accentuated male characteristics such as pinnae and cervical apteria;
2. territorial possession - males only boomed from their territories but could boom from any portion of it;
3. individual identity - 'listless tooting' in late mornings appeared to be characteristic of individuals;
4. aggressive state - 'booming parallel' was usually given near a territorial edge and was probably indicative of a tendency to attack; 'listless tooting' occurred more freq-

uently from centers of territories and conveyed a low likelihood of attacking.

The primary functions of booms and booming displays are to attract birds to booming grounds and to particular territories. Although it is more useful to attract hens, it may be advantageous to also attract males if a combination of signals from several males acts as a supernormal stimulus or beacon in guiding hens. While booms are especially useful as long range attractants (they can be heard over 2-3 km; Hamerstrom and Hamerstrom, 1960), booming displays are more useful in short range communication.

Booms and booming displays may also function in territorial maintenance and as tonic signals (sensu Schleidt, 1973). Booming parallel, for instance, appeared to be directed at other males and the forward posture of booming displays signifies aggression. As tonic signals, booms can maintain status quo among males and reduce overt aggression. Individual recognition is helpful in this respect if it helps distinguish neighbors from strangers. Most (Hamerstrom and Hamerstrom, 1960; Sharpe, 1968; Hjorth, 1970) concur that booms and booming displays are polyvalent.

Whines and cackles

Whines and cackles convey ambivalence between staying and leaving. Both vocalizations occurred most frequently when ambivalence was high as, for example, when predators or danger was near, in intense agonistic situations or in flutter jumps when new birds arrived.

Possible functions of whines and cackles include alerting other birds of danger, attracting hens to a male's territory via flutter

jumps and territorial defense. The alarm function is supported in that whines and cackles from a disturbed bird usually were contagious. Flutter jumping is an unambiguous visual signal which locates a male precisely and the accompanying vocalizations may help alert females. During agonistic bouts, more vigorous cacklers appeared likely to attack (thus the high association between cackles and agonistic behaviors). Hence, these calls may signify a high likelihood of attacking.

Stamps, whoops, flutter jumps and nuptial bows

These behaviors were given only by males. They were associated with each other by cluster analyses and were most frequent when females were likely to visit. Thus, they appear to contain information concerning sex and reproductive status of individuals. They may also pinpoint a signaling male.

Functionally, flutter jumps differ from the other behaviors in that jumps better locate a male and are used more often in mate attraction between 20-50m. Males most frequently flutter jumped when hens were 2 or more territories away but changed to stamping and whoops when females were in or near their territories. In contrast, nuptial bows only occurred when a hen was in a territory for several minutes. The dichotomy is not absolute, however, for whoops can be heard over 1-2 km and may help attract hens to a booming ground. Nuptial bows are particularly interesting in that they are antithetical to forward displays. Thus they dissolve hostilities between sexes and facilitate copulation. Although there is general agreement

that flutter jumps, stamps, and bows are primarily epigamic, Hjorth (1970) believed that whoops were mostly agonistic while Hamerstrom and Hamerstrom (1960) and Sharpe (1968) cited epigamic functions for this call.

Forward displays, face offs and stand offs

Forward postures and displays were given by both sexes but were performed most frequently by males in early season when territories were being established. They probably indicate various levels of aggressive tendencies. For example, forward postures alone denote a relatively low likelihood of attacking and a high tendency to withdraw. Increasing likelihood of attacking is demonstrated by forward rushing--running parallel--stand offs--face offs. The undisputed functions of these behaviors are to establish and maintain territories.

Other behaviors

Walking, comfort movements and semi-alert are low priority behaviors that contain little information. Some forms of walking (e.g. retreating from an agonistic situation), however, may indicate submission and some comfort movements may be displacement behaviors or redirected aggression. Upright alert may warn others of potential danger but appears to be less effective than whines or cackles.

Sharptail displays

Dancing, chilks and cork notes

Characteristics of these behaviors include: high association with each other in time and by cluster analysis; greatest frequency

during peaks of hen visitations; directionality; and limitation to males. Thus they indicate sex, location and reproductive status of signalers.

Their primary functions are epigamic. Chilks and, less frequently, dancing could be heard for 1-2 km under favorable conditions and may attract hens to dancing grounds and to specific territories. Cork notes were softer and are probably limited to short range mate attraction. In addition, all 3 behaviors are aggressive among males and function in territorial defense. Hjorth (1970) emphasized that dancing, chilks and cork notes were 'intensively aggressive' but Lumsden (1965) cited both aggressive and epigamic functions for these displays. Kermott and Oring (1975) described them as epigamic displays that have been ritualized from aggressive acts.

Coos

Coos were similar to prairie chicken booms in their weak association with other behaviors, frequent occurrence (particularly in mid-spring) and limitation to territorial males. Unlike booms, however, coos were virtually absent when hens were present. Coos, therefore, contain information about sex, territorial and possibly social status of a signaler but not about reproductive status or individual identity. Some low-level aggressive information may also be given by the forward posture of cooing displays.

Perhaps the most important function of coos and cooing displays is as a tonic signal. By serving as constant vocal and visual reminders or 'place holders', they may maintain territories and minimize

overt aggression. They may also advertise a dancing ground's location but are not as effective as chिल्s in this respect. In general, all functions mentioned here except tonic signaling were supported by Lumsden (1965), Hjorth (1970) and Kermott and Oring (1975).

Gobbles

Although gobbles were most closely associated with coos, gobbles occurred more frequently in early spring when territories were being established. Aggressive females gobbled at other hens on dancing grounds (Lumsden, 1965; Kermott and Oring, 1975) and males gobbled most frequently at edges of territories. Calls of males may be individually characteristic. Therefore, gobbles denote aggressiveness, individuality and perhaps social status but not sex or reproductive condition.

The most apparent function of gobbles among males is territorial maintenance (Lumsden, 1965; Kermott and Oring, 1975). Individual recognition could assist in this function if distinguishing between neighbors and strangers reduced overt aggression. Among hens, the vocalization may permit more aggressive birds to copulate first. Hjorth (1970), who did not observe sharptails during the period of territory establishment, concluded that this highly aggressive signal was a low priority activity.

Whines and cackles

Although these calls are structurally homologous to those of prairie chickens, they contain very different information. Sharptail whines and cackles only occurred in agonistic situations and were

most intense immediately before fighting. Thus, they indicate a high likelihood of staying in place (rather than ambivalence) and attacking. Their most important functions are establishment and defense of territories.

Other sharptail and hybrid displays

Forward displays, nuptial bows and comfort movements carry similar information as homologous prairie chicken behaviors. As far as can be discerned, information and functions of displays in hybrids are directly comparable to those of corresponding activities in parental species. Whines and cackles of hybrids occurred in the same situations as those of prairie chickens and probably indicate ambivalence rather than a determination in remaining.

Stereotypy in Prairie Grouse Displays

Wiley (1973) analyzed the strut display of sage grouse males and found that many temporal components had extremely low variability, often with coefficients of variation (CV) of 1.5 or less. Vocalizations were less stereotyped in frequency characteristics, but, their variability may have been due to differing orientations to microphones. No mention was made of other aspects of stereotypy such as completeness or consistency between successive events. Wiley argued that high stereotypy is important in highly polygynous species that have brief courtship. In these species, redundancy may interact with low variability to provide precise species-specific signals with clearly communicated meanings. Communally displaying species of grouse, therefore, should be consistent in these characteristics.

Greater prairie chicken booming displays and sharptail dancing, however, were noticeably more variable than sage grouse strutting and few prairie grouse vocalizations were extremely stereotyped. Only strongest frequencies of booms and coos had CV's near 1.0 for combined samples. Variation within individuals was occasionally less than group variation (e.g. CV's in note duration in booms of some birds were less than 1.5 and less than 1.0 in some temporal characteristics of particular prairie chicken cackles) but prairie chicken and sharp-tail behaviors in general were not temporally stereotyped. Therefore, it is important to discuss why temporal stereotypy is not common in these species.

First, high CV's in prairie grouse displays suggest that the measured characteristics may not be normally distributed but follow logarithmic normal or Poisson distributions (Schleidt, 1974). A CV of 1.00, for example, would suggest a Poisson distribution and independence of events. This is particularly pertinent to temporal features of booming and dancing displays in that many of the characteristics had CV's near unity and independence would imply that succeeding acts were not related in time. Also, if some characteristics were log-normally distributed, they could still be highly stereotyped (Schleidt, 1974). Distributions were not examined, however, due to small sample sizes and because it appeared that prairie grouse relied on other forms of stereotypy.

Second, Wiley may be incorrect in assuming that courtship in communally displaying grouse is only marginally long for species recognition. As he indicated, females spend 4 or more mornings

visiting a display ground before copulating. Svedarsky (personal communication) and I have found similar situations among prairie grouse in our study area. Four days may not differ substantially from premating contacts in birds with more conventional mating systems and pair bonds. This is probably long enough to permit identification of conspecific males and this time may well be used to select a male of superior fitness.

Third, while low temporal variability is uncommon in prairie chicken and sharptail displays, other forms of stereotypy such as repetition of single acts, predictability of sequencing and degree of completeness are obvious. For example, booms, whoops, chilks and cork notes were at least moderately repeated. Stamps, booms, whoops; and dances, chilks and cork notes were associated in transition matrices with a high likelihood of a given behavior following any other. This evidence and preliminary Markov chain analyses suggest a high predictability in sequencing when hens are present. Finally, all analyzed booming and dancing sequences that were filmed when hens were present contained identical elements but those from periods without females lacked aspects such as stamping, pinnae elevation or calls.

Information Overlap in Prairie Grouse Signals

In addition to high redundancy and repetition in whines, booms, whoops, chilks and corks, prairie grouse exhibit considerable overlap in information among acoustical and visual signals. Information redundancy frequently facilitates signal transmission when high background noise interferes with transmission in 1 or more modal-

ities. It is apparent that display grounds can be very noisy areas, particularly when an individual attempts to convey information concerning itself. The following section discusses this overlap and its significance in both species.

Functional overlap in prairie chickens

The greatest amount of overlap in prairie chicken displays is between stereotyped booming displays and booms; whines and cackles; and whoops and stamps. Some overlap may occur among forward displays and between face offs and stand offs, but these behaviors form continua and are more graded than overlapping.

Although booms may be more effective in long range communication, they share considerable information with stereotyped booming displays. Both indicate that a male is on his territory and in reproductive condition. Duplication of information in this pair of behaviors may help transmit vital information to conspecifics, particularly females, through noisy channels. It is critical for a male to attract hens away from nearby males, and, rather than relying on only one channel, males utilize both that are available.

Stamping and whoops help identify locations of males while conveying some of the same information present in booms and booming displays. Because they are limited to periods of high sexual motivation, however, stamps and whoops share greater overlap with each other than with booms and booming displays. Apparently, overlap has similar purposes in both pairs of behaviors.

Whines and cackles, although polyvalent, are not epigamic and seem less important in identifying specific males. Thus, their func-

tional overlap does not appear to be a result of noisy backgrounds but rather as a means of preventing habituation in a manner suggested by Hartshorne's (1973) monotony threshold. Although this theory has been criticized (e.g. Dobson and Lemon, 1975; Krebs, 1976) and alternative theories for switching have been suggested (e.g. Krebs, 1977), the concept that switching may reduce habituation to frequently repeated signals still appears valid. Bursts of cackles frequently interrupted long, agonistic and alarm bouts of whines when habituation was most likely and may have served to re-alert antagonists or neighbors.

Functional overlap in sharptails

Sharptail displays with significant overlap include dancing, cork notes and chilks; whines and cackles and gobbles and coos. The interpretation of whines and cackles is identical to that of prairie chickens and need not be expounded.

Dancing, with both acoustical and visual aspects, chilks and cork notes have information concerning sex, breeding status, location and motivation of signaler. They are also closely associated and occur when competition for information transfer is highest. The overlap in these behaviors, therefore, may be a strategy to increase signaling efficiency in a very noisy medium.

Gobbles and coos are frequently given together, as evidenced by the transition matrix. While these vocalizations have some different functions, both are at least partially aggressive. In this case, switching may be a result of a sharptail monotony threshold. Alternatively, it may indicate rapidly changing ambivalence between different degrees of aggression in agonistic behavior.

Functional overlap in hybrid displays

Because the Pankratz hybrid behaved like a prairie chicken, overlap in its coom and cooming displays, stamps and whoops and whines and cackles is interpreted like that of corresponding prairie chicken behaviors. The WTymp hybrid was interesting in that it may have reduced overlap in its large repertoire by switching between prairie chicken and sharptail behaviors in appropriate circumstances.

Possible Constraints on Prairie Grouse Vocalizations

The physical range of vocalizations within a species is usually limited in comparison to the total range of its family. Constraints on these ranges may be related to anatomy or environment. Anatomical constraints are involved primarily in syringeal musculature and related structures and should be similar among closely related species. Environmental factors may include excess attenuation by the habitat and competition with other sounds coming from conspecifics, other species or abiotic factors (e.g. thermal turbulence, wind or waterfalls). Because biotic competition is described elsewhere, only anatomical and abiotic constraints are discussed here.

Anatomical constraints

The simple vocal apparatus of prairie grouse closely resembles that of domestic chickens except for larger resonating chambers produced by cervical air sacs (Johnsgard, 1973). Because of this simple structure, the trachea and pharynx have little resonating abilities and most grouse vocalizations have undampened harmonics. Some modification is possible with bifurcated syrinxes, air sacs and muscles.

The major effect of the air sacs in prairie grouse is to increase resonance of booms and coos (Johnsgard, 1973). The larger chambers of prairie chickens result in greater resonance which decreases the fundamental frequency of booms. Resonance and some muscle control may also dampen harmonics, making booms, coos and whoops relatively pure tones. In addition, bifurcated syrinxes can act independently so that 2 fundamental frequencies and associated harmonics can be produced simultaneously (Greenewalt, 1968). This phenomenon may account for the complex frequency structure of chिल्s, gobbles and some whines. In general, however, the relative simplicity of grouse vocal apparati greatly reduces the range of their vocalizations and results in raucous and noisy calls.

Environmental constraints

Morton (1975) and Wiley and Richards (1978) showed that grasslands are poor acoustical media. Excess attenuation is high in these areas because of thermal turbulence, high winds and absorption. Morton (1975) suggested that to counteract this attenuation, grassland birds should either display in the air or have vocalizations with low carrier frequencies. Another possibility is to vocalize when some of the attenuating factors are reduced.

Probably because of high energetic costs of flying in species with high wing loading, prairie grouse have only 1 aerial display - the flutter jump. However, the display probably has not evolved to increase the carrying power of whines and cackles. Rather, the vocalizations appear to combine with jumping to help advertise a

male's location. Support for these statements includes: 1) sharptails do not vocalize while jumping; 2) whines and cackles also occur while a male sits or stands; and 3) even while he sits, a male's vocalizations travel long distances. In short, aerial displaying appears unimportant in long distance signal transmission in these species.

Many prairie grouse vocalizations, particularly booms and coos have low fundamental frequencies which may help in broadcasting. Coos, however, do not travel as far as booms due to decreased amplitudes at their source. Whoops, chilks and gobbles also travel well, frequently carrying farther than coos (Oring, personal communication).

Crepuscular activity may help signal transmission because wind and thermal turbulence are decreased at twilight. Although predation has sometimes been cited as a factor responsible for crepuscular activity, diurnal predators have insignificant effects on displaying grouse (Berger et al., 1963; Spärling and Svedarsky, 1978) and nocturnal predators such as great horned owls (Bubo virginianus) may counteract any advantages of early morning displaying. Thus, circadian rhythms of prairie grouse may center around a strategy that maximizes signal transmission.

Coding of Species-specificity in Prairie Grouse Displays

Both hypotheses concerning the coding of species-specificity (i.e. similar agonistic and dissimilar courtship displays) (Marler, 1957) seem to hold for prairie grouse displays. The dichotomy is not perfect, however. In this section structures of displays are examined in relation to interspecific communication.

Agonistic displays

The most obvious similarities in the agonistic displays of prairie grouse are forward displays, face offs, stand offs and overt fighting. Except for occasional wing elevation in sharptails, the displays are virtually identical among both parental species and hybrids.

Gobblers are exceptions to Marler's hypothesis in that they are given by sharptails and hybrids but not by prairie chickens. A 'gobble-like' vocalization in the lesser prairie chicken (Sharpe, 1968) may be homologous to sharptail gobbles. If so, it raises some interesting questions concerning the phylogeny of Tympanuchus-Pedioecetes and the evolution of prairie grouse signals. Perhaps greater prairie chickens secondarily lost gobbles from their repertoires. Spectrograms of lesser prairie chicken gobbles also slightly resemble greater prairie chicken booms, however, and further research must be conducted before the phylogeny of gobbles can be determined.

Epigamic displays

Epigamic displays are more difficult to interpret as species isolaters than agonistic behaviors for several reasons including: 1) they are involved in both intraspecific sexual recognition and species-specificity; 2) some characteristics of these displays contain both sets of information, others only 1; 3) natural selection may have operated at different rates on the 2 species; and 4) many displays that are primarily epigamic have other functions and may be less different interspecifically than expected. The most intriguing be-

haviors include stereotyped booming, cooing and dancing displays and their associated sounds.

Less stereotyped forms of booming and cooing displays are similar in form and contain information that a male is present and has at least some tendency to defend a territory. Border disputes between males on mixed display grounds frequently involved reciprocal booming and cooing parallel and it is likely that heterospecifics detected some of the aggressiveness in the other species' visual displays. Booms and coos, however, are very different and could be more important in transmitting species identity.

Stereotyped forms of booming displays are clearly epigamic and must be compared to sharptail dancing. These displays have few similarities, as would be predicted. Although stamping, forward posturing, tail swishing and air sac inflation are in both, qualitative and temporal aspects of these displays are sufficiently different to avoid confusion. Although stereotyped booming and dancing also may have some aggressive functions, these purposes are not as pronounced as courtship and were probably less effective in shaping the displays.

The vocalizations analyzed with discriminant analysis also support Marler's hypotheses and illustrate the confounding effects of polyvalency. Whoops and chilks are primarily epigamic and were not misclassified between species. Because prairie chicken whines and cackles are polyvalent, they have some features (e.g. most frequency characteristics) that are species-specific and others that allow interspecific communication of aggressive intentions. While most whines were correctly classified, a few were not, suggesting that some in-

formation may be transmitted between species. It is significant that cackles, which appear to be more aggressive than whines in both species, had the largest percentage of misclassified samples.

Females are apparently very capable of recognizing con- from heterospecifics, based on a 1-4% rate of hybridization (Johnsgard and Wood, 1968; see pp. 174-180), a high affinity for conspecific territories on mixed grounds and avoidance of hybrid males (see pp. 183-186). If hens utilize characteristics that convey both sexual and species identity, prairie chicken hens should prefer large, orangish apteria; long pinnae; short stamping bouts; and long booms and whoops while sharptail hens should prefer group synchronized dancing; extended wings; small, purplish apteria; loud, extended stamping; short, high-pitched chिल्s and cork notes. Testing these preferences provides an area for exciting future research.

Temporal and contextual coding

Prairie grouse displays with comparable functions are similar between species in their daily and seasonal occurrences. Dancing, chिल्s, cork notes, whoops and stampings peaked during periods of hen visitations while aggressive displays peaked in early spring when territories were formed and decreased as territories stabilized. Many of the polyvalent displays including coos, booms and whines remained high throughout most of the season. Thus, differences in daily and seasonal occurrence of displays are insufficient to be species-specific. These displays also have similar associations with each other in both species and, except for coos and booms, hetero-

specific males differ only slightly in their use of homologous displays.

Behavioral Genetics in Prairie Grouse

Behaviors of hybrids can be used to determine some display components that are primarily under genetic control. Components that are found in most F1 hybrids and retain parental characteristics are probably dominant traits; those which differ among hybrids should be pleiotropic. This analysis is limited in that genetic foundations for displays common to both species (e.g. *formal displays*) or those that are recessive cannot be determined from this limited sample. Although hybrids and parental species may be able to modify some of their behaviors through experience (Sparling, in press), the extent of this ability appears limited to only a few components of some signals and has little bearing on inherited aspects.

The presence of gobbles, whoops, pinnae and a boom or coo vocalization are probably dominant traits for all F1 and backcross hybrids had them. Pinnae elevation is more ambiguous than presence of pinnae because even sharptails raised their hackles above cervical apteria when displaying; motor patterns may be homologous even though feather modification is limited to 1 species. The ability to coo may be inherited independently of booming for the Pankratz hybrid only gave 1 vocalization (coom) while the WTymp male gave both coos and cooms.

While the ability to give these displays may be dominant, their quality appears to be pleiotropically determined. For instance, gobbles, whines, cackles and whoops of the Pankratz and WTymp hybrids

differed in several characteristics from each other and from parental species. The duration and strongest frequency of hybrid coos were clearly intermediate between parental species but frequency modulation and amplitude were very different. Angle of wing elevation, duration of stamping, body marking, pinnae length and number of apertures were intermediate between both parental species and may have been due to incomplete dominance.

Pleiotropy and incomplete dominance may be important in maintaining species integrity in that blending of behavioral traits in male hybrids may have repulsed females. Blending in female hybrids did not appear to be as important for a hybrid female was actively courted and copulated by a male prairie chicken.

Summary

Information content, functions, species-specificity and other aspects of prairie grouse signals were examined in detail. Greater prairie chicken and sharp-tailed grouse forward displays, face offs and stand offs and sharptail gobbles are intraspecifically aggressive. Other behaviors including prairie chicken booming displays, booms, whoops and stamping and sharptail dancing, cork notes, chilks and coos are either epigamic or polyvalent. Corresponding hybrid displays have similar functions as those in parental species.

While temporal stereotypy is not common in prairie grouse displays, other forms of stereotypy including redundancy, completeness of epigamic displays and posturing are common. Although Wiley's (1973) arguments for temporal invariability were rejected for these

species, other forms of stereotypy outlined by Schleidt (1974) may facilitate signal transmission through noisy media.

Signal transmission is further enhanced by information redundancy and functional overlap between acoustical and visual modalities. Booming displays and booms in prairie chickens, for example, convey similar information but increase the likelihood of the message reaching its 'intended' target (i.e. a female) by using 2 channels. Sharptail dancing, chilks and cork notes also overlap.

Prairie grouse vocalizations are constrained by anatomical and environmental factors. Simple vocal apparati result in harmonically complex, noisy vocalizations with the exceptions of booms and coos which may be modified by resonating chambers in cervical air sacs. Grass-land environments are poor acoustical media and prairie grouse compensate for high excess attenuation by having low carrier frequencies in major vocalizations and by being crepuscular.

In general, prairie grouse displays adhere to Marler's (1957) hypotheses regarding coding of species-specificity. Most agonistic displays are similar between species although gobbles are an exception. Epigamic displays are confounded by polyvalency and sexual selection but tend to differ between species. Particularly important, sharp-tails have 2 displays for courtship and maintenance of status quo among males while prairie chickens have essentially 1 for both functions. Temporal and seasonal occurrence of displays and interbehavioral relationships appear unimportant in species isolation.

Comparisons among hybrids and parental species suggest genetic bases for some displays. The ability to gobble, whoop and give a

boom/coo - like vocalization seems to be under the control of dominant genes but the expression of these behaviors and cackles, whines, stamping, wing elevation and chilking are probably regulated pleiotropically. Some morphological characteristics such as body markings, length of central rectrices and pinnae, and color and size of cervical apteria are influenced by blending due to incomplete dominance or pleiotropy. The blending of parental characteristics may be an important factor in species isolation as females seem to avoid hybrid males.

SECTION 3

PRAIRIE GROUSE RESPONSES TO INTRASPECIFIC PLAYBACKS

Numerous studies (see, for example, Brown, 1975; Smith, 1977) have shown experimentally the importance of vocalizations in avian communication. Although these studies have used a variety of taxa, most have only looked at passerines and only a few have tested call notes. Because non-passerines usually rely on calls rather than song, current knowledge of avian communication may be biased towards 1 order of birds.

Greater prairie chickens and sharp-tailed grouse are 2 tetraonids that have well-developed vocal repertoires. Both sharptail (e.g. Evans, 1961; Lumsden, 1965; Kermott and Oring, 1975) and prairie chicken (e.g. Schwartz, 1945; Hamerstrom and Hamerstrom, 1960; Sharpe, 1968) displays have been described and compared (e.g. Grange, 1940; Hjorth, 1970). Most of these studies, however, were strictly descriptive and only that by Kermott and Oring (1975) used controlled playback experiments.

The objectives of this study were to determine intraspecific functions of primary vocalizations and to develop a basis for comparing between-species responses to these calls. This study reports only on results obtained from within-species playbacks.

Methods and Materials

Playback experiments were conducted from 1 half hour after arrival of males to their departure in peak seasons of prairie grouse activity (mid April to late May) from 1975 to 1978. All playbacks occurred when females were absent.

Nagra DH speaker-amplifiers were placed within territories of subject males and calls were played with a Uher 4000 Report-L tape recorder. On most mornings, 2 speakers were used on different parts of display grounds to reduce risk of habituation. Playback amplitude was standardized with a General Radio model 1565A sound level meter at 95 dBA, slow needle response, at a distance of 1 meter from the source.

Tests consisted of three 3-minute periods of preplayback, playback and postplayback. During these periods, 15 prairie chicken and 19 sharptail behaviors were recorded in field notes in shorthand notation. Because many of these behaviors were rare, only the most common were used in analyses.

Playback order was randomized for each male and at least 10 minutes separated successive trials. All playbacks were conducted when birds surrounding the subject male were inactive so as to minimize their influence on the subject's responses. Possible habituation was checked by replaying a call that earlier had elicited obvious responses; there were no noticeable differences in reactions between first and second playbacks in any of these checks.

Prairie chicken playbacks included booms, stamps, whoops, cackles, whines and composite calling. Sharptail sounds included coos, gobbles, cackles, 2 types of dancing (5 and 20 chirps per second,

respectively), whines, chilks, cork notes and composite calling (see Lumsden, 1965; Kermott and Oring, 1975; and pp. 41-75 for descriptions of these displays). Composite calling in each species included epigamic sounds made on a display ground when a female was present and included a continuous series of booms, whoops, whines and cackles from prairie chickens; and, dancing, cork notes and chilks from sharptails.

Activity rates were computed from the 3-minute behavioral samples and compared to indices of activities for each species. These indices (Appendix V) were similar to "hybrid indices" used by Emlen (1972) and were calculated from mean activity rates taken from 5-minute focal animal samplings recorded every 20 minutes throughout the season. A score of "zero" for an index category meant that the bird gave less than half the mean number of acts during that period. A score of "1" meant that between 0.5 and 1.5 the mean number were given and "2" meant that more than 1.5 times the mean number of acts were given.

Because there were no significant differences among years (Mann-Whitney U Test, $p > 0.10$), the data were combined. Index scores were tested among periods using Friedman 2-way and Kruskal-Wallis 1-way analyses of variance (Siegel, 1956). Although the Kruskal-Wallis test is less appropriate than the Friedman for related samples, it usually offered a conservative check on statistical significance. Only those playbacks found significant with both tests are discussed in detail.

Most birds were individually recognizable. Six prairie chickens were banded, 2 others were the only chickens on a mixed ground at the time of testing and the rest (0 to 5, depending on test) had distinctive markings (see Hamerstrom and Hamerstrom, 1973 for examples of these marks) and occupied stable territories remote from other subjects. Similarly, 9 sharptail males were banded, 1 limped and the rest (0 to 8) had distinctive markings and stable territories. There was little possibility that 1 or 2 birds may have been tested twice with the same call.

Results

Prairie Chicken Responses to Playbacks

Prairie chickens reacted significantly to booms, whines, whoops and composite calling (Table 22.A). In each case, playback periods had higher mean scores than either pre- or postplayback. Composite calling may have elicited the strongest responses for the difference between means of playback and the other periods was greatest for this recording.

Detailed responses (Fig. 26) showed that prairie chicken reactions to booms were weak; most activities between pre- and playback periods were reduced and only alert increased. Playbacks of whines elicited additional whines and alert responses. They may have slightly inhibited booms initially but appeared to evoke them after a short refractory period in postplayback. Composite calling tended to elicit booms, stamps, whoops and alert responses. Major responses to whoops were increased whines and alert and decreased stamping; cessation of whoops may have caused birds to decrease booming.

TABLE 22

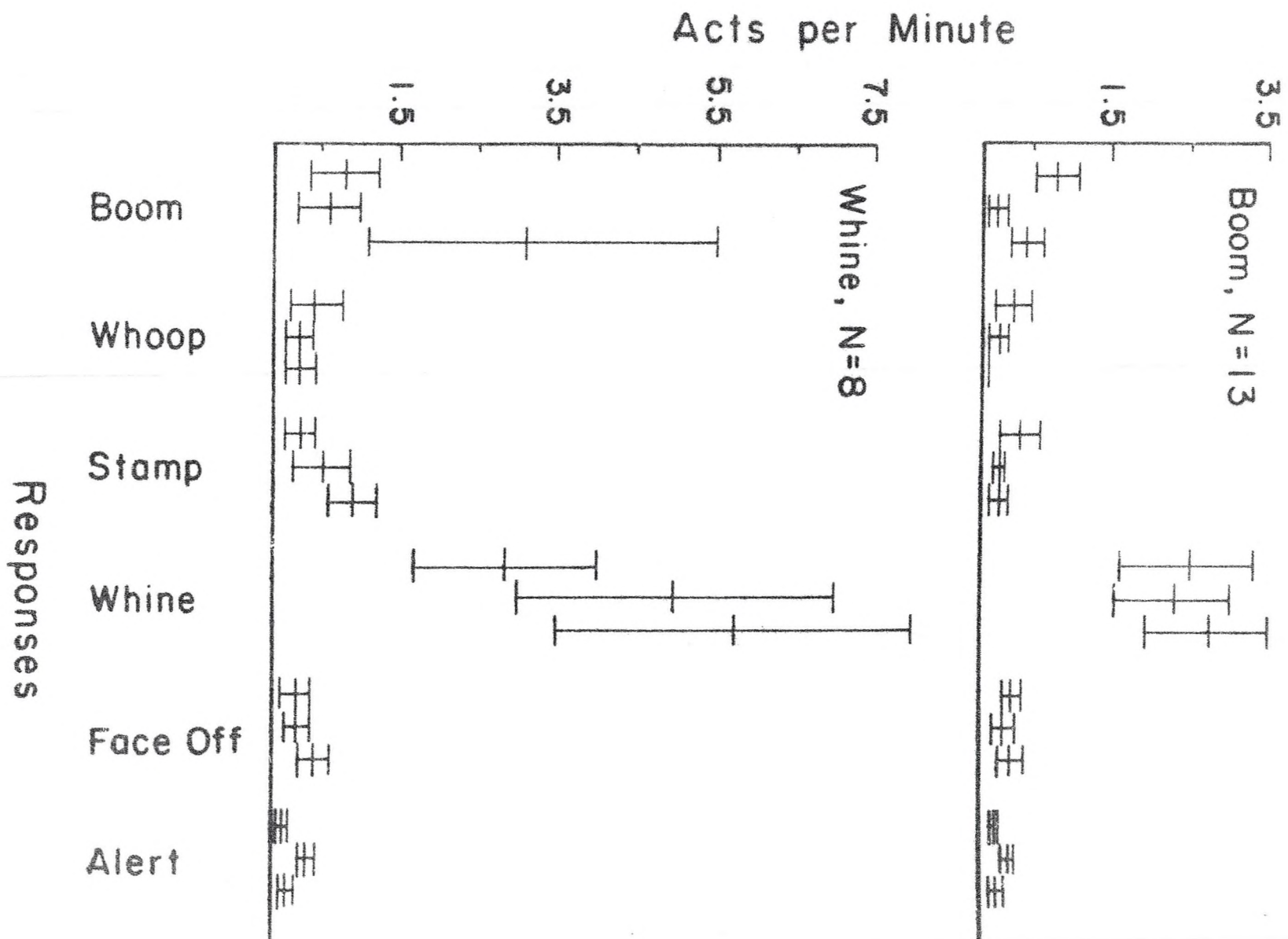
MEAN BEHAVIORAL INDEX SCORES OF MALE PRAIRIE GROUSE
RESPONSES TO CONSPECIFIC PLAYBACKS

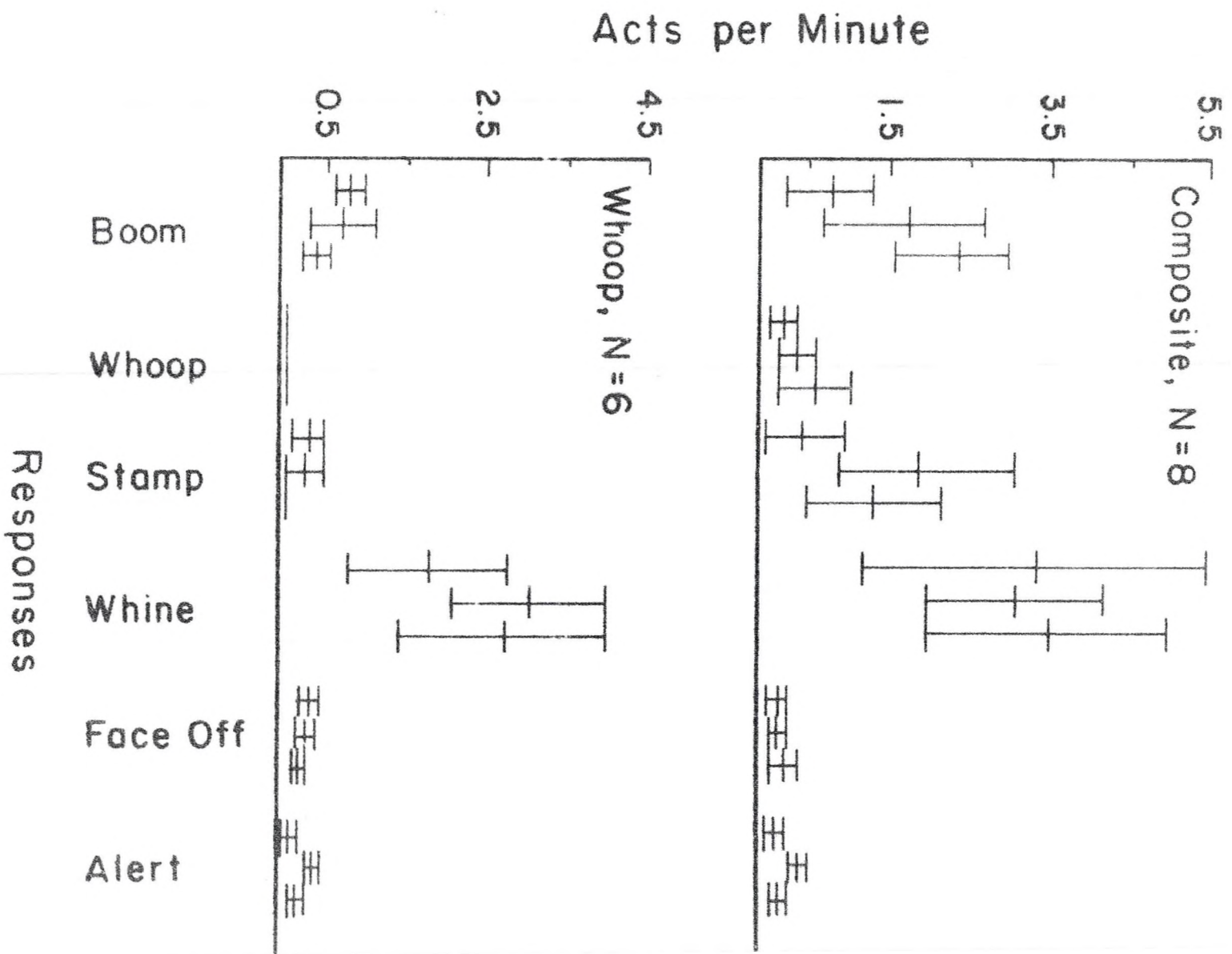
Call	N	Pre	Dur	Post	$\chi_r^2^a$	Sig.	H ^b	Sig.
A. Responses of Prairie Chickens								
Boom	13	2.46	2.92	2.08	26.79	0.001	20.64	0.001
Whine	8	2.12	3.50	2.62	6.63	0.05	2.72	n.s.
Composite	8	1.12	5.00	3.00	10.19	0.005	9.98	0.01
Stamps	6	2.33	2.67	2.17	1.08	n.s.	0.25	n.s.
Cackle	8	2.75	3.62	3.12	3.05	n.s.	0.00	n.s.
Whoop	6	1.00	3.50	1.50	8.00	0.16	5.62	0.05
B. Responses of Sharptails								
Coo	18	2.17	4.11	2.11	12.11	0.01	12.15	0.01
Cackle	9	2.44	2.11	1.44	6.78	0.05	7.58	0.02
Chilk	10	2.30	3.69	1.90	8.75	0.02	7.01	0.05
Cork Notes	6	1.67	4.50	2.50	8.08	0.03	6.79	0.05
Composite	9	1.55	3.78	2.22	4.22	n.s.	4.25	n.s.
Gobble	10	1.70	4.70	3.10	12.60	0.01	7.79	0.05
Whine	9	1.33	2.55	1.55	2.67	n.s.	1.73	n.s.
Dance	11	4.36	5.83	3.91	6.04	0.05	7.60	0.05
Dance-Chilk	12	3.58	4.42	3.25	2.17	n.s.	5.67	n.s.

^a χ_r^2 = Friedman 2-way ANOVA statistic.

^b H = Kruskal-Wallis 1-way ANOVA statistic.

Figure 26. Detailed responses of prairie chickens to intra-specific playbacks. Values include means (center bars) and one standard error. In each group of three, the first line represents rates for preplayback, the second for playback and the third for postplayback.





Responses of Sharptails to Playbacks

Significant differences in sharptail responses were elicited by coos, cackles, gobbles, chilks, cork notes and low-chilk dancing (Table 22.B). In comparison to the other periods, playback sessions had the highest scores in every case except cackles. Based on differences in mean scores between playback and other periods, gobbles and cork notes appeared to elicit stronger responses than other sounds.

Playbacks of coos significantly increased coo and gobble rates and slightly depressed chilks and face offs (Fig. 27). Chilks increased coos and alert, reduced chilks during playback but may have resulted in an increase in chilks during postplayback. Cackles inhibited most behaviors except alert; coos, dancing and chilks were most noticeably depressed. Playbacks of cork notes increased coos and elicited gobbles and alert responses. Gobbles most strongly evoked coos and gobbles but may have also increased dancing and alert. Dancing with few chilks elicited gobbles and alert responses, may have produced additional coos and inhibited face offs. In contrast, dancing with many chilks only increased alert behavior and resulted in decreases of other activities.

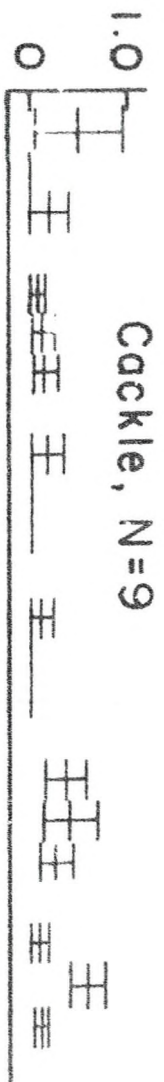
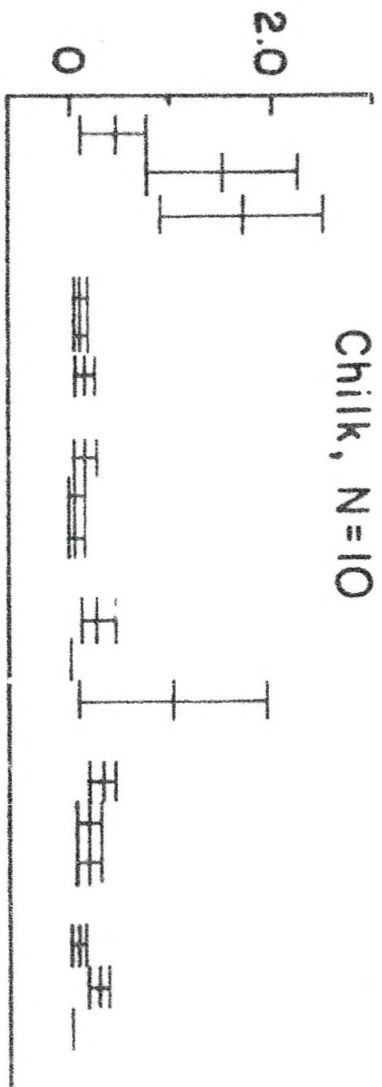
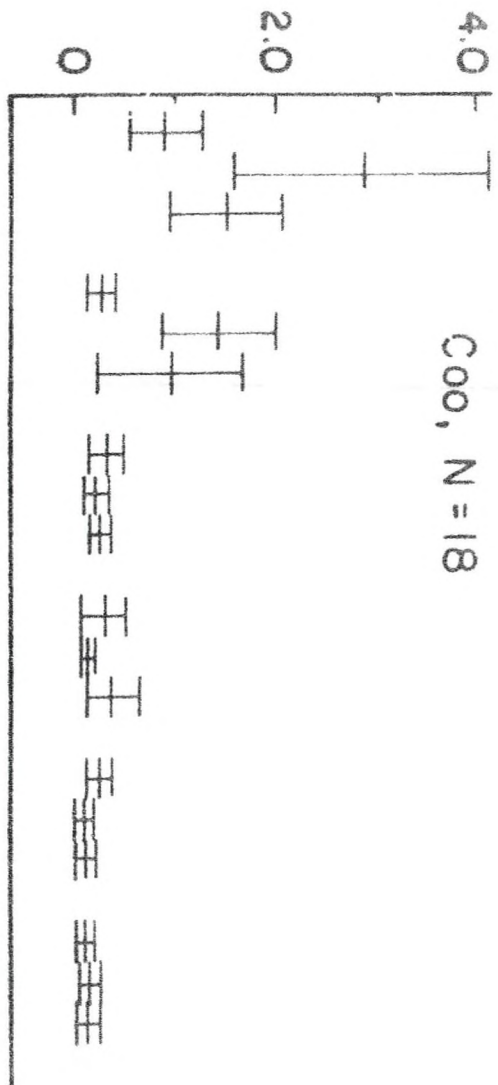
Discussion

Functions of Prairie Chicken Sounds

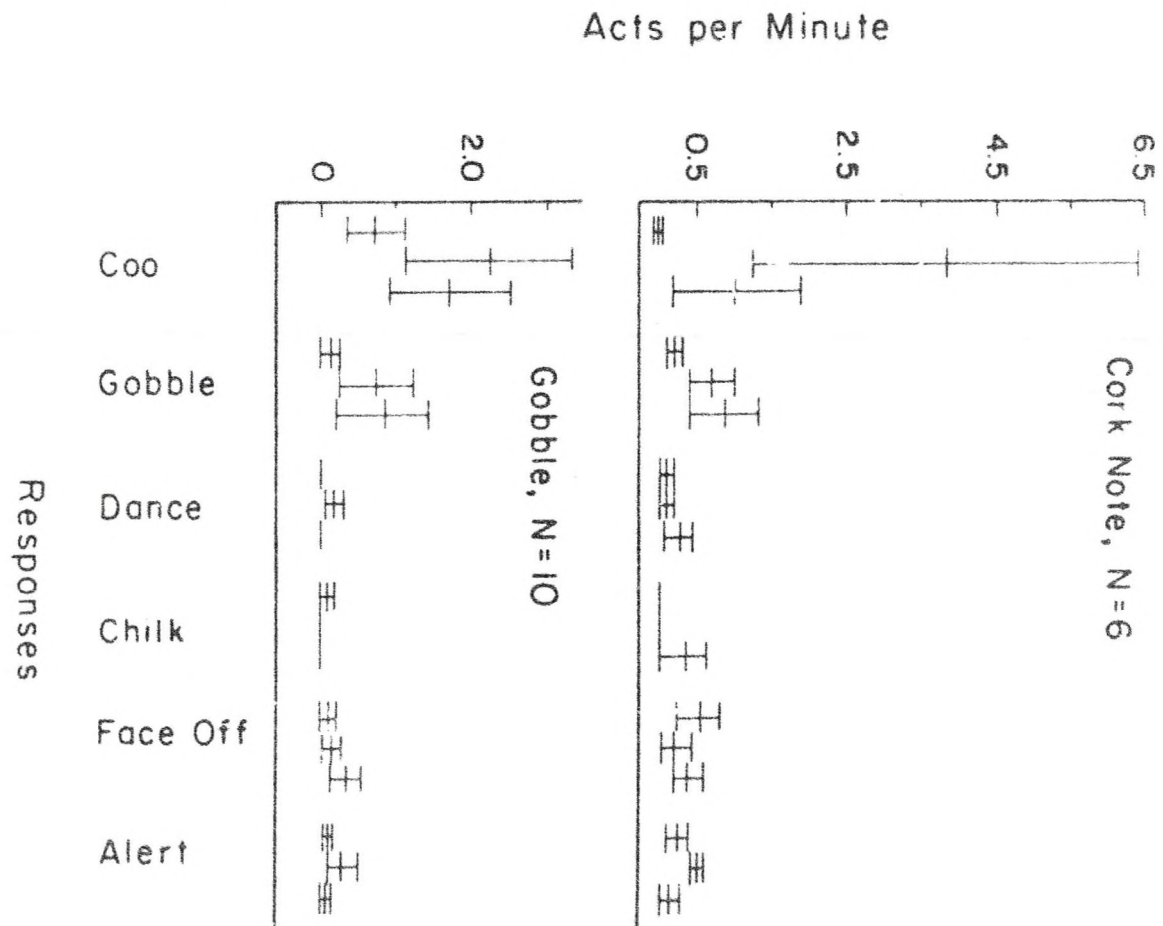
In most instances, hypotheses based on contextual data were confirmed by experiments. For example, reciprocal alarm was proposed as a function of whines and whines and alert responses increased with playbacks of whines. Decreases in booms and other displays during

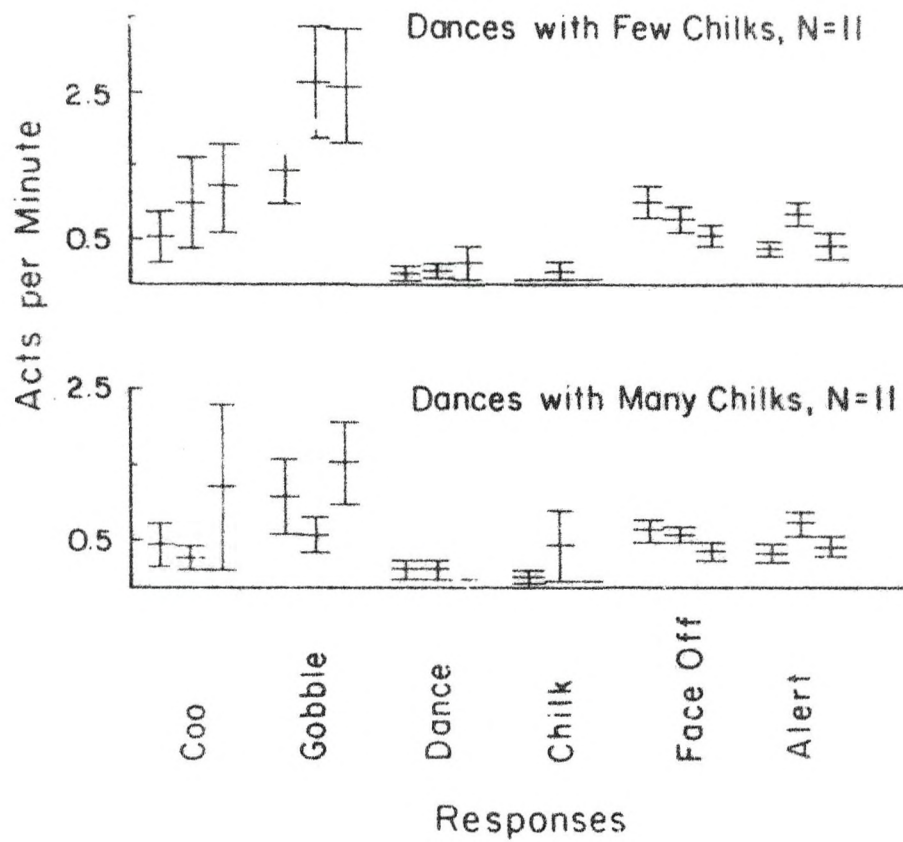
Figure 27. Detailed responses of sharptails to intraspecific playbacks. Values include means (center bars) and one standard error. In each group of three the first line represents preplayback, the second playback and the third postplayback.

Acts per Minute



Responses





playbacks of whines may be explained in that alarm signals should arouse birds and decrease most of their activities.

As playbacks of booms had only a slight inhibitory effect on most other activities and no appreciable effect on the behaviors of a lone male (Hamerstrom and Hamerstrom, 1960), it is unlikely that booms play a major role in direct intermale communication. This evidence indirectly supports the tonic signal and mate attraction functions previously cited (see pp. 115-116). Under natural conditions, visual signals of a booming male may be more important between males or they may synergize with acoustical signals for intra- and intersexual communication.

Composite sounds initially elicited alert responses but later increased epigamic displays such as booms, whoops and stamps. They were also very effective in attracting males to display grounds after flushing or walking off and have been used to lure males for trapping (Silvy and Robel, 1967). This combination of sounds may serve as a Gestalt of an active group of prairie chicken males and probably signals that a female is present. Hearing these sounds, males are attracted and begin to court.

Because the only responses to whoops were slight rises in alert behavior and whines, this vocalization appears to have little function in intermale communication. Circumstantial evidence suggests that whoops are primarily epigamic but may have a slight aggressive function. Hamerstrom and Hamerstrom (1960) played whoops to a lone prairie chicken male and found that it boomed and flutter jumped.

Booms and whoops together only elicited a small amount of booming in their experiments. A lone male might respond more vigorously to a conspecific epigamic signal than a group of males if his responses attracted conspecifics. The combined stimuli from additional males could help attract females.

Functions of Sharptail Sounds

Playbacks of coos and gobbles had similar effects in eliciting additional coos and gobbles and in decreasing epigamic displays. Therefore, these vocalizations probably have agonistic functions. Based on contextual evidence, however, gobbles are more aggressive than coos. Coos were given primarily by peripheral males or by birds within the relatively safe centers of their territories but gobbles were given most frequently at territorial borders. In addition, coos peaked after territories had been established while gobbles were most frequent when aggression was highest in early season (Kermott and Oring, 1975; see pp. 94-98). Lumsden (1965) and Hjorth (1970) suggested that coos and gobbles were both very aggressive among males. Kermott and Oring (1975), however, stated that coos were primarily involved in advertisement and that gobbles were the major call denoting aggression. Kermott and Oring also showed that gobbles contain information about the identity of the caller. My findings support those of Kermott and Oring except that I would place more weight on an aggressive function of coos.

Chilks occurred during courtship and probably function in attracting mates. Playbacks also indicated that chilks were mildly

aggressive among males because they noticeably increased coos. Other observations support the aggressiveness of *chilks*; sharptail males occasionally *chilked* during obviously aggressive forward rushes and running parallels and directed these calls at antagonists. Lumsden (1965) and Hjorth (1970) described *chilks* as aggressive. Kermott and Oring (1975) stated that they are ritualized forms of aggression that are used in courtship. My findings support both aggressive and epigamic functions. Cork notes occurred in courtship but also may communicate aggression in that their playbacks greatly increased coos and gobbles.

Based only on playback results, cackles appeared to have little function in intermale communication. However, of all the calls tested, cackles were most out of context. Under natural conditions, they are virtually restricted to intense, close-encounter disputes. Thus, cackles may evoke very different responses when played from a speaker than when coming from a nearby male. Crouching may be an appropriate response to loud, intensively aggressive signals with no recognizable source.

Dancing with few *chilks* evoked aggressive responses probably because it is the form most commonly occurring in agonistic displays. Dancing with *chilks* and composite sounds, both reminiscent of courtship dancing, did not elicit significant responses from males and are probably more important in intersexual communication. Kermott and Oring (1975) consistently elicited dancing with playbacks of dancing but they did not state if *chilks* and cork notes occurred on their tapes. I tried at least 5 versions of dancing without eliciting

similar responses from males. Under natural conditions, dancing is obviously contagious among males on the same display ground. Future research may determine the significance of dancing in intermale communication.

Interspecific Comparisons

With the exception of cackles, sharptails responded more vigorously to conspecific vocalizations than did prairie chickens. For example, sharptail responses to coos, chilks, gobbles and cork notes were more blatant than prairie chicken responses to booms, whoops and whines. The reasons for this difference are not clear, but they may be related to species-specific differences in aggression as suggested by Ammann (1957). My studies indicated that sharptails spent proportionately more time in aggressively oriented activities than prairie chickens (see pp. 94-98). It appears, therefore, that sharptails are more aggressive than chickens, at least intraspecifically.

In general, the only major difference between prairie grouse call notes and passerine song is that grouse require more signals to convey similar messages. Prairie chickens, for example, indicate that a male is on his territory and in reproductive condition by booming and whooping while sharptails do it by cooing, chilking, dancing and giving cork notes. Each of these signals, however, also conveys specific information unique to it. Other features of song including individuality and dialects have already been suggested for prairie grouse vocalizations (Kermott and Oring, 1975; Sparling, in press).

Summary

Functions of prairie grouse vocalizations were tested with playback experiments. In general, these experiments supported interpretations based on contextual data. Prairie chicken whines are contagious alarm calls, composite sounds are strong attractants of males and females, and booms and whoops appear more important in intersexual than in intermale communication.

Sharptail coos, gobbles, chilks, cork notes and stamping elicit aggressive responses although the last 3 may also be involved in courtship. Cackles have little effect except to decrease most behaviors. This call is viewed as a highly aggressive signal that was played at a very high amplitude.

Sharptails seemed to react more strongly to conspecific signals than did prairie chickens. The reasons for this difference may be related to higher aggressive levels in sharptails but the factors behind the higher aggression are unknown.

SECTION 4

ETHOLOGICAL ISOLATING MECHANISMS IN PRAIRIE GROUSE

II. EXPERIMENTS WITH MALES

Ethological isolating mechanisms are probably the most widespread and important factors maintaining integrity between sympatric, closely related species (Mayr, 1963). Of many aspects involved in species isolation, communication frequently is of greatest significance. In birds, for instance, acoustical signals maintain species integrity in Vermivora warblers (Gill and Lanyon, 1964; Ficken and Ficken, 1968 a,b,c; Murray and Gill, 1976), meadowlarks (Lanyon, 1957; Rohwer, 1972) and buntings (Emlen, 1972; Shiovitz, 1975). Visual signals function in geese (Cooke and McNally, 1975; Cooke, 1978) and other waterfowl (Johnsgard, 1960, 1963), thrushes (Dilger, 1956) and finches (Zann, 1976). Frequently, a combination of acoustical and visual cues are used.

In this study, ethological isolating mechanisms between greater prairie chickens and sharp-tailed grouse are experimentally examined. More specifically, visual recognition of females and discrimination of con- and heterospecific vocalizations by males are tested.

A study of reproductive isolation between these species is valuable for they share a narrow belt of sympatry through which a low level of hybridization occurs (Johnsgard and Wood, 1968). Moreover, descriptions of their displays (Hamerstrom and Hamerstrom, 1960;

Hjorth, 1970) show that while some agonistic behaviors are similar, courtship displays tend to differ between species. This suggests that both types of behavior may be important in keeping the species apart.

Methods and Materials

Playback experiments followed the same procedures outlined above (see pp. 137-139). In brief, prerecorded vocalizations were standardized at 95 dBA with a General Radio 1595A sound level meter and played through Nagra DH speaker-amplifiers using a Uher 4000 Report-L tape recorder. Two speakers were usually used to avoid habituation. Tests consisted of three 3-minute periods of preplayback, playback and postplayback during which 15 prairie chicken and 19 sharptail activities were recorded in shorthand notation. Playback order was randomized for each male and at least 10 minutes separated trials. Computed activity rates were compared to behavioral indices (Appendix V) for each bird and the 3 periods were statistically contrasted with Friedman 2-way and Kruskal-Wallis 1-way analyses of variance (Siegel, 1956).

In 1975 and 1976, several natural experiments occurred when females of either species visited a mixed display ground. At these times, behaviors of 7 prairie chicken and 12 sharptail males were sampled over 5-minute periods and analyzed for differences between 2 periods of a hen present (con- or heterospecific) and a period taken in early morning when no female was present.

To determine if prairie grouse males could distinguish the species of females by plumage characteristics alone, a few experiments

were conducted in which mounts of females in the copulatory position were placed in male territories. Reactions of males were noted upon their arrival in early morning.

Results

Male Responses to Live Females

Male prairie chickens differed significantly among periods of prairie chicken hens, sharptail hens and no hen present in the rate of forward rushes ($p < 0.01$), booms ($p < 0.01$), stamps ($p < 0.002$), whoops ($p < 0.04$) and walking ($p < 0.007$) (all tests were 1-way ANOVA'S) (Table 23). A posteriori comparisons (Tukey's test, $p < 0.05$) showed that stamps and whoops differed between periods of prairie chicken hen and sharptail hen, booms differed between no and either female present and walk was highest when sharptail hens were present (Table 24).

Sharptail males differed among periods in face offs ($p < 0.02$), dances ($p < 0.001$), chilks ($p < 0.001$), cork notes ($p < 0.001$) and marginally in gobbles ($p < 0.07$) (Table 25). A posteriori comparisons (Table 26) showed that chilks differed among all groups, cork notes and dances between no female and either female and face offs between prairie chicken and sharptail hen presences.

Male Responses to Decoys

Although prairie chicken males showed no significant differences in responding to con- or heterospecific hens ($p > 0.10$, chi-square, Table 27), sharptail males responded much more actively to conspecif-

TABLE 23
ACTIVITY RATES OF PRAIRIE CHICKEN MALES
WHEN FEMALES ARE PRESENT

		Acts Per Minute									
		Face Off	Forward Rush	Stand Off	Whine	Fight	Boom	Stamp	Whoop	Walk	Comfort
Species of Female Present											
Prairie Chicken ^a (N = 21)	\bar{X}	0.18	0.69	0.29	8.82	1.54	11.83	11.28	5.96	0.05	0.00
	SE	0.06	0.16	0.06	2.12	0.95	0.88	1.25	1.75	0.03	0.00
Sharptail (N = 9)	\bar{X}	0.18	0.22	0.37	8.04	0.22	8.63	6.37	2.07	0.33	0.22
	SE	0.15	0.11	0.14	2.69	0.11	0.97	1.28	0.76	0.11	0.15
No Female (N = 18)	\bar{X}	0.18	0.18	0.24	14.56	0.07	8.21	5.84	1.44	0.10	0.22
	SE	0.06	0.07	0.08	2.60	0.04	0.88	0.97	0.49	0.05	0.11

^aSample size refers to number of samples taken.

TABLE 24

A POSTERIORI COMPARISONS OF RESPONSES BY
MALE PRAIRIE CHICKENS TO FEMALES

Behavior ^a	Prairie Chicken	Sharptail	No Female
Face Off			
Forward Rush			
Stand Off			
Whine			
Fight			
Boom			
Stamping			
Whoop			
Walk			
Comfort			

^aLines connect groups whose means cannot be considered as coming from independent populations ($p < 0.05$, Tukey's test).

TABLE 25

ACTIVITY RATES OF SHARPTAIL MALES
WHEN FEMALES ARE PRESENT

		Acts Per Minute								
Species of Female Present		Face Off	Forward Rush	Stand Off	Gobble	Whine	Coo	Dancing	Chilk	Cork Notes
Sharptail ^a (N = 22)	\bar{X}	1.06	0.31	0.25	1.56	1.41	1.94	4.13	11.61	6.23
	SE	0.17	0.09	0.10	0.73	0.46	0.85	0.55	2.42	1.08
Prairie Chicken (N = 6)	\bar{X}	0.87	0.28	0.00	0.14	0.00	1.11	5.37	24.64	4.18
	SE	0.32	0.22	0.00	0.11	0.00	0.91	0.82	5.46	2.26
No Female (N = 25)	\bar{X}	0.46	0.21	0.09	3.98	0.89	3.74	1.18	1.19	0.83
	SE	0.12	0.07	0.04	0.98	0.50	1.04	0.51	0.44	0.43

^aSample size refers to number of samples taken.

TABLE 26

A POSTERIORI COMPARISONS OF RESPONSES BY
MALE SHARPTAILS TO FEMALES

Behavior ^a	Sharptail	Prairie Chicken	No Female
Face Off	_____		
Forward Rush		_____	
Stand Off	_____		
Gobble	_____		
Whine	_____		
Coo	_____		
Dance	_____		
Chilk			
Cork Notes	_____		

^aLines connect groups whose means cannot be considered as coming from independent populations ($p < 0.05$).

TABLE 27
MALE PRAIRIE GROUSE RESPONSES TO HEN DECOYS

Species of		Number of Male Responses			
Male	Mount	Court	Copulate	Ignore	Total
PC	PC	4	3	2	9
PC	ST	2	2	4	8
ST	PC	0	0	10	10
ST	ST	4	3	8	15

ics. No significant differences were found between the 2 species' responses to conspecifics.

Responses to Heterospecific Playbacks

Prairie chickens had significantly higher index scores to sharptail coos, cork notes and composite calls and marginally significant scores to gobbles (Table 28). The strongest responses to coos included alert behavior and whines and slightly decreased booms and face offs (Fig. 28). Gobblers markedly decreased whines and slightly increased booms and alert. Cork notes elicited the strongest responses by significantly increasing booms, alert, stamps and whine responses. Playbacks of composite calls elicited similar responses except that booms did not increase appreciably. Sharptails decreased all behaviors except alert in response to playbacks of prairie chicken cackles (Table 28).

Discussion

As in many avian species, prairie grouse appear to rely on visual and acoustical cues for species isolation. Visual signals, for instance, are important in distinguishing con- from heterospecific females. Particular features responsible for this discrimination may include breast, belly and facial markings, length of pinnae and central rectrices or subtle behavioral cues.

Sharptail males appear less responsive to heterospecific visual signals than do prairie chickens. This decreased responsiveness is evident in 2 respects. First, although tests with decoys

TABLE 28
BEHAVIORAL INDEX SCORES OF MALE PRAIRIE GROUSE
RESPONSES TO HETEROSPECIFIC PLAYBACKS

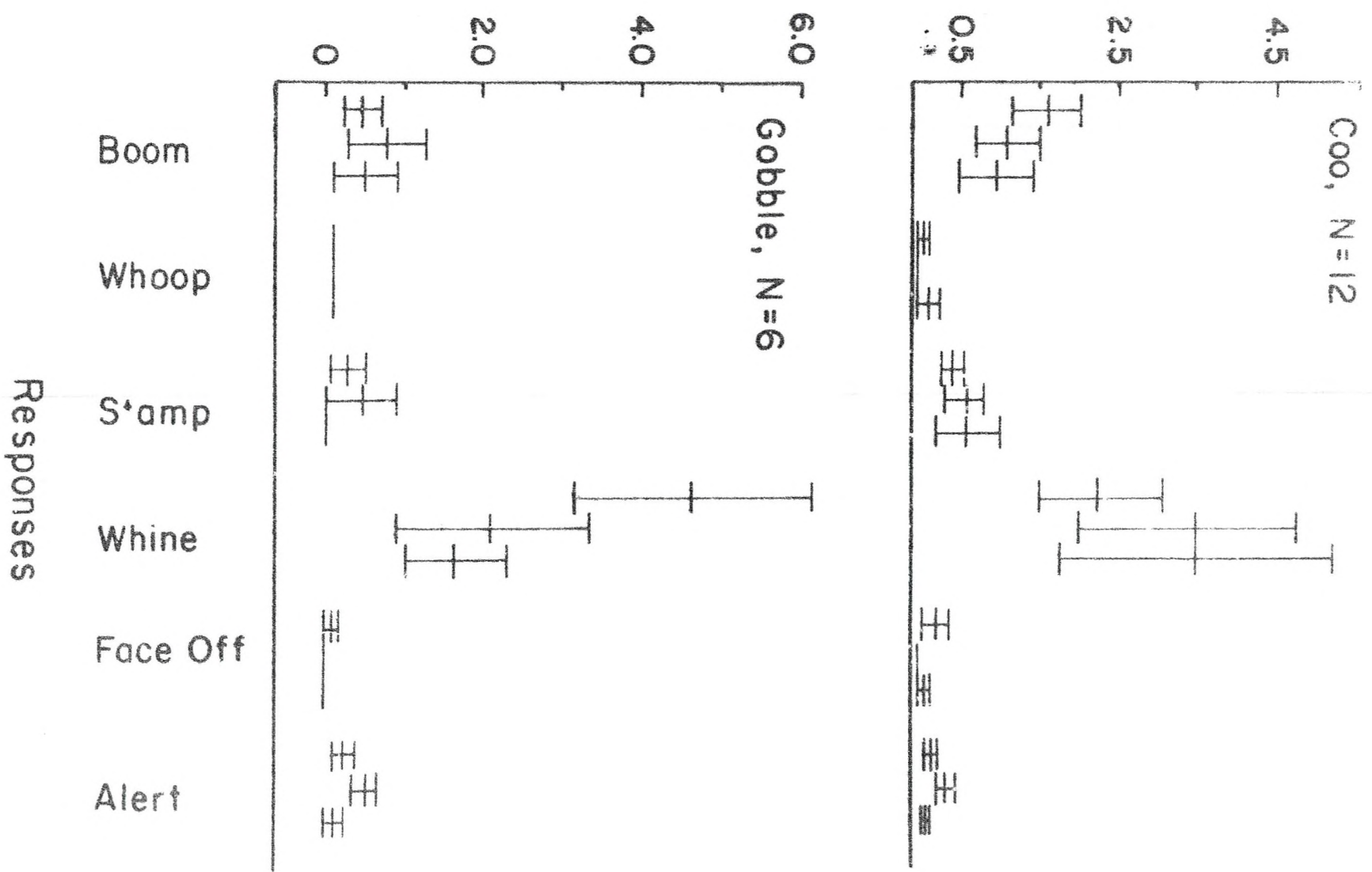
Call	N	Pre	Dur	Post	$\chi^2_r^a$	Sig.	H ^b	Sig.
A. Responses of Prairie Chickens								
Coo	12	2.12	3.50	1.00	12.79	0.01	12.46	0.01
Gobble	6	1.33	2.17	0.83	6.08	0.05	3.50	n.s.
Dancing	5	1.60	1.80	1.60	0.40	n.s.	0.00	n.s.
Cork	5	0.60	2.80	0.80	7.60	0.02	9.35	0.01
Chilk	5	0.40	1.00	1.00	0.70	n.s.	0.33	n.s.
Whine	5	1.20	1.60	0.40	2.10	n.s.	3.39	n.s.
Composite	6	1.50	3.33	0.83	8.58	0.12	6.61	0.05
B. Responses of Sharptails								
Boom	16	2.37	2.75	1.94	1.22	n.s.	1.98	n.s.
Cackle	5	1.80	2.60	0.60	6.40	0.04	4.99	0.07
Whine	5	2.60	2.00	1.40	1.60	n.s.	1.59	n.s.
Stamp	8	2.12	4.12	2.12	5.69	n.s.	4.58	n.s.
Composite	5	2.40	2.60	2.60	0.10	n.s.	0.02	n.s.
Whoop	6	3.00	4.17	2.83	1.58	n.s.	1.60	n.s.

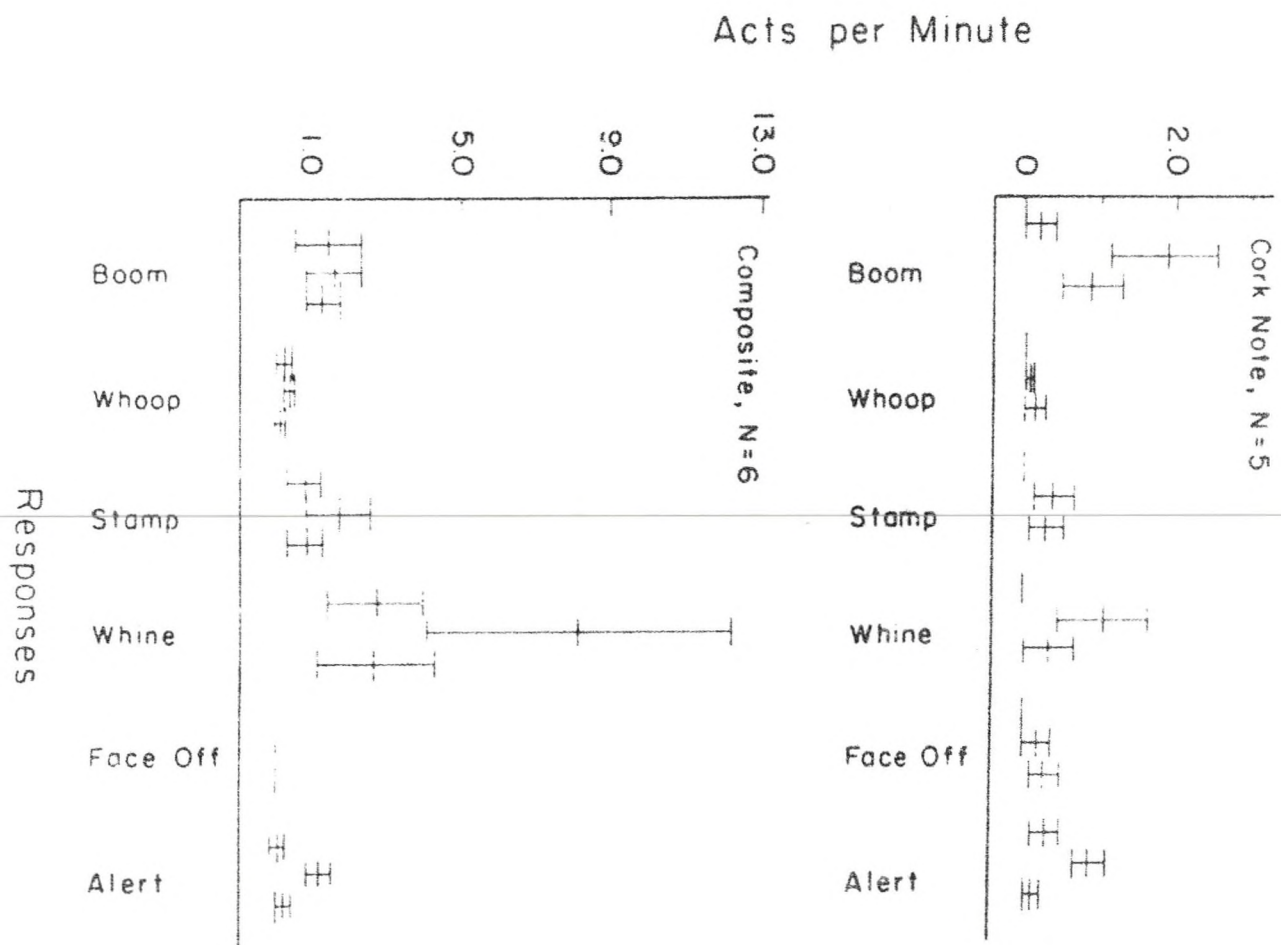
^a χ^2_r = Friedman 2-way ANOVA statistic.

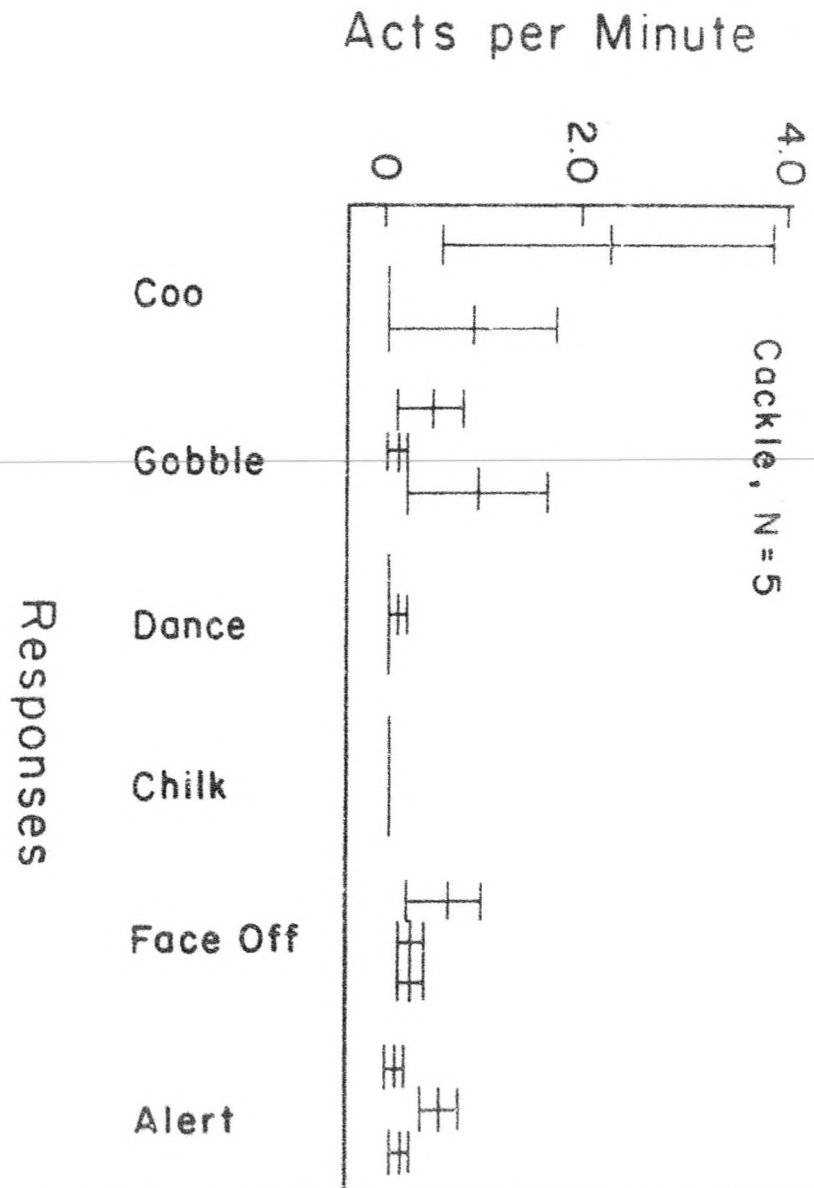
^b H = Kruskal-Wallis 1-way ANOVA statistic.

Figure 28. Detailed responses of prairie chickens and sharp-tails to interspecific playbacks. Values include means (center bar) and one standard error. In each group of three the first line represent preplayback, the second playback and the third postplayback.

Acts per Minute







indicated that prairie chicken males courted and copulated with hens of either species, sharptails only responded to conspecifics. Second, while males of both species differed in their response to live con-, heterospecific and no hens, field observations indicated that there were greater interspecific differences than revealed by activity samples. Sharptail males, for instance, frequently ignored prairie chicken hens on a mixed ground, even when a hen walked through a male's territory. Prairie chicken males, however, always courted sharptail hens and frequently flew 75m from their territories to females, even if this led to aggressive encounters and chasing by sharptail males (hence the significant increase in walking).

Acoustical displays may be important in spacing heterospecific males in that prairie chickens responded appropriately to aggressive signals of sharptails. Coos, gobbles and cork notes, which elicited aggressive responses from sharptails (Kermott and Oring, 1975; see pp. 148-151), evoked excitement or alarm whines, alert behaviors and/or agonistic displays from prairie chickens. Composite sounds, although not eliciting significant responses from sharptails, resulted in aggression in prairie chickens. It is particularly interesting that cork notes and gobbles, which are not given by prairie chickens, elicited aggressive responses from them.

Sharptails responded only to prairie chicken cackles, which are structurally similar to their conspecific homolog. In sharptails, the call has very aggressive functions and occurs only in territorial disputes. Thus, crouching and alert responses to prairie chicken

cackles may be appropriate behaviors to very intense, highly aggressive signals coming from an unknown source. As with visual displays, sharptails seemed far less receptive to heterospecific acoustical stimuli than did prairie chickens.

Decreased receptivity of sharptails to heterospecific stimuli may be due to past sympatry with other closely related species including greater prairie chickens, ruffed grouse (Bonasa umbellus), sage grouse, spruce grouse (Canachites canadensis), blue grouse (Dendragapus obscurus) and willow ptarmigan (Lagopus lagopus). Greater prairie chickens, on the other hand, have had only limited contact with sharptails and possibly ruffed grouse, lesser prairie chickens (which may be conspecific, Short, 1967) and sage grouse. Assuming that intraspecific competition is greater than interspecific, selection may favor increased sensitivity for conspecific stimuli in those species that live sympatrically with several close relatives. Reproductive and aggressive energies may thus be channelled more efficiently.

Species recognition is not restricted to the outline above. Female sharptails, for instance, frequently gobbled and clucked when visiting display grounds (Lumsden, 1965; Kermott and Oring, 1975) while prairie chicken hens seldom vocalized. Therefore, female vocalizations may be useful in discriminating species. Similarly, sharptail males may use similar visual characteristics for recognizing prairie chicken males and females. Certainly, visual aspects of courtship displays are sufficiently different to aide males in distinguishing other con- and heterospecific males.

Summary

Greater prairie chicken and sharptail males were tested for their ability to discriminate con- from heterospecifics with live females, female decoys and playbacks of male vocalizations. While males of both species differentially responded to live females, observations indicated that sharptails responded significantly less to heterospecifics than did prairie chickens.

Prairie chicken males responded to sharptail coos, gobbles, cork notes and composite sounds. Most of these responses were indicative of alertness, excitement or aggression. Sharptails responded only to prairie chicken cackles but in a way identical to their own call. Differences in prairie chicken and sharptail responses to heterospecific stimuli may be related to greater historical contact between sharptails and confamilials.

SECTION 5

ETHOLOGICAL ISOLATING MECHANISMS IN PRAIRIE GROUSE. III. MATE SELECTION BY FEMALES

Two theories have been proposed for mate selection in birds. The oldest, postulated by Darwin (1871) states that an individual (usually, but not always a female) should select a mate with characteristics indicative of superior fitness. This form of sexual selection leads to development of conspicuous secondary sexual characters and/or epigamic displays. Adherents of this theory include Sibley (1957), Selander (1972), Cooke and McNally (1975) and Weatherhead and Robertson (1977a).

The other theory states that individuals should select mates with superior territories. Implicit in this theory is that potential mates defend variably amounts of a necessary resource. This theory forms the basis for the Verner-Orians model (Verner, 1964; Orians, 1969) and is supported by Zimmerman (1966), Verner and Engelson (1970), Holm (1973) and Caccamise (1977). Weatherhead and Robertson (1977b), however, have argued against it being an important factor.

These theories are not exclusive and in practice both may explain a particular situation. Characteristics such as aggressiveness and dominance, for example, may simultaneously allow an individual to obtain a high-quality territory and serve as mate attractants.

Both theories have been postulated for the highly skewed reproductive success enjoyed by central prairie grouse males (Lack, 1939; Schwartz, 1945; Lumsden, 1965; Robel, 1966; Wiley, 1973; Ballard and Robel, 1974; Robel and Ballard, 1974). Most authorities have found that central males are the most aggressive and oldest birds on the display grounds (Robel, 1972; Hamerstrom and Hamerstrom, 1973). Therefore, females may rely on characteristics which either indicate male status or improve with maturation. Alternatively, males and females may independently select central territories and male characteristics may have little direct influence on female choice.

The purpose of this section is to determine female preferences for con- and heterospecifics in greater prairie chickens and sharp-tailed grouse and to relate these preferences to the 2 theories stated above. Although this study was conducted in captivity, results indicate what may happen in the wild.

The study of female mate selection is critical to the understanding of reproductive isolation in these species, for, try as they may, prairie grouse males are unable to copulate unless a hen is receptive. Thus, hybridization is ultimately due to female choice. In addition, females have a much greater investment in a brood and, if hybrids have reduced viability or fertility, selection should favor strong species recognition in this sex.

Methods

All birds used in this study were raised in captivity from eggs. Prairie chickens came from deserted or partially depredated nests in northwestern Minnesota; sharptails were second or third

generation captive birds from the same area. In 1976 a prairie chicken male was crossed with a sharptail hen and the resulting F1 hybrids were backcrossed in 1977. Backcross progeny are referred to as 3/4 prairie chickens (= prairie chicken x F1 hybrid) or 3/4 sharptails (= sharptail x F1). All territorial males were at least 2 years old. Some females were virgins, others had mated the previous year. All were individually marked with colored and numbered leg bands.

Birds were housed together from hatching, first in a battery brooder and then in a barn connected to a 15.2 x 45.7m wire mesh enclosure. Both sexes were kept together from early summer through winter and separated in April before the breeding season began. This group housing was maintained to challenge the strength of species recognition by hens. Observations over 3 years indicated that breeding chronology of captive birds lagged behind that of wild birds by 2 weeks.

In April, 8 prairie chicken, 11 sharptail and 4 hybrid males were released into the enclosure to establish territories. Only 3 males of each parental species and an F1 hybrid male did so. All non-territorial males except 3 of each parental species, which served as controls on the importance of territory possession, were then removed.

Males were filmed at 5 to 8 secs/frame using 2 Nizo S80 movie cameras with clocks set in the center of the cameras' views. Prairie chicken behaviors were divided into booming, whoop and/or stamp, forward, agonistic, neutral (standing, walking, eating) and unidentified categories. Sharptail categories included active and quiet dancing, agonistic, neutral and unidentified. Some categories overlapped

slightly but, in general, boom, whoop and/or stamp, active and quiet dancing were epigamic displays while forward and agonistic categories were mostly aggressive.

All experiments occurred between 05:15 and 07:30 from 10 to 21 May 1978. Females were ushered in pairs from the barn into a runway which opened into the enclosure (Fig. 29). They were not handled at this time but some were encouraged to move by hand waving. Once hens were in the enclosure, their positions were located on a grid at 10 second intervals for periods usually lasting 10 minutes. Occasionally females which appeared receptive but hesitant were kept in the enclosure for up to 20 minutes. Support posts along the sides and center of the enclosure aided in locating females. If females did not copulate during a period, they were separated and retested on subsequent mornings. Some hens were never receptive.

In the following account 2 aspects of female preference were measured. The first, or initial preference, is the amount of time a hen spent in a male's or species' territory. It was statistically compared to expected values based on the relative sizes of these territories. The second aspect, or ultimate choice was the male (or species) a hen copulated with. Throughout "PC" stands for prairie chicken and "ST" for sharptail.

Results

Female Aspects

Prairie chicken hens spent 99.5% of their time in conspecific territories (Table 29). This was significantly greater than expected

Figure 29. Diagram of the interior of test enclosure. Dark rectangles are shelters not included in the computation of male territory size. Dark circles are center posts used as guides in determining female locations. Dotted lines delineate areas frequently occupied by non-territorial males.

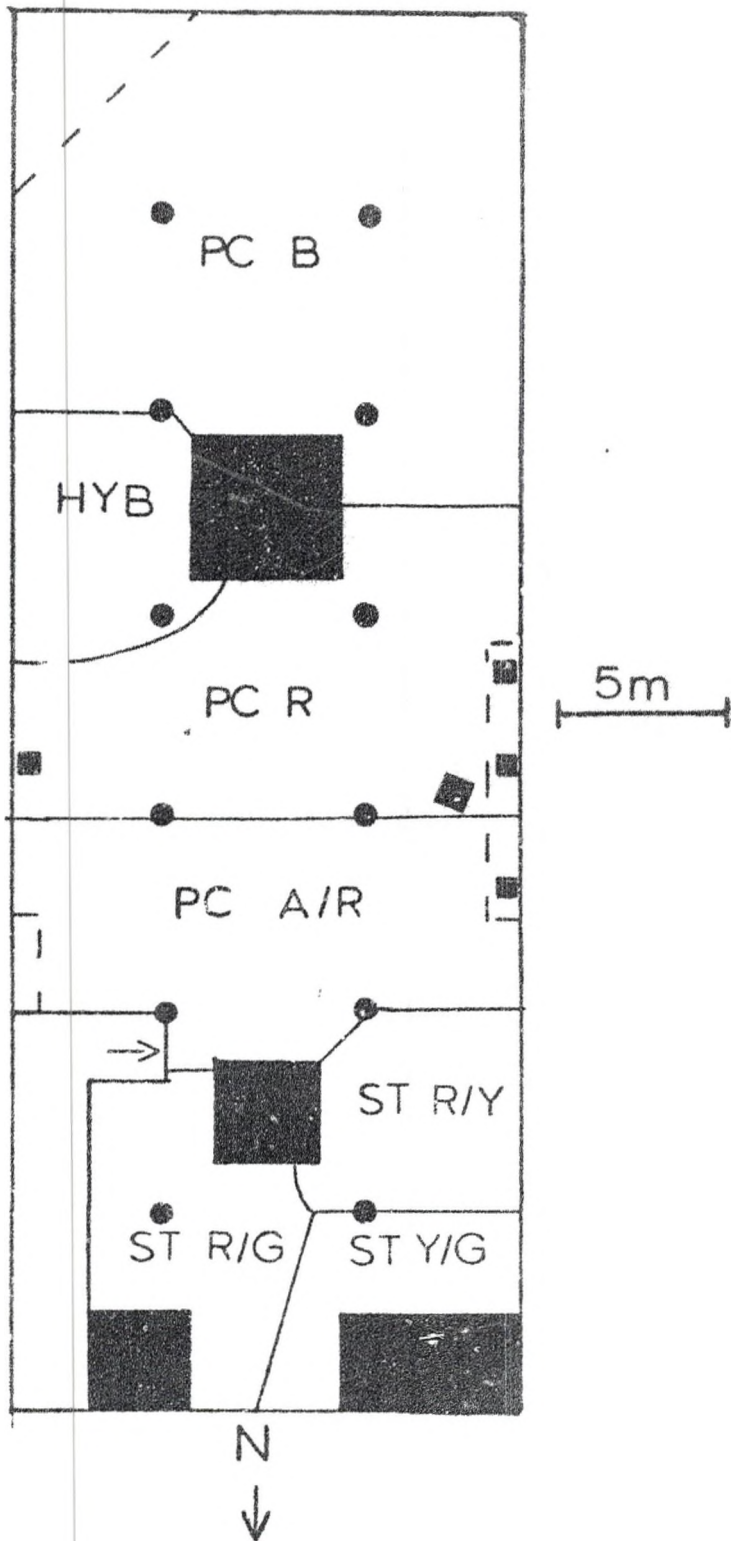


TABLE 29
MATE SELECTION BY FEMALE PRAIRIE GROUSE

		Percent of Time Spent in Males' Territories							Mated Date ^a	Sample Time (min.)
Female	Species	PC B	PC R	PC A/R	F1	ST R/Y	ST Y/G	ST R/G		
R32	PC	85.7	14.3					PC R	10	4.83
R2	PC			100.0				PC A/R	10	0.50
R72	PC	94.1	4.6	0.6				0.6 ———		31.00
R69	PC		95.0	5.0				PC R	10	10.00
R99	ST	19.0	50.8			2.4	27.8	———		20.00
R35	ST		20.6	16.4	0.6	14.2	32.0	16.2 ST R/Y	16	54.75
R56	ST	3.2	31.9	20.7	13.1	20.7	8.4	1.9 ST R/Y	20	30.50
W65	ST	45.0	5.2	31.2		4.3	0.4	13.9 ST R/G	16	10.50
R9	ST	14.1	8.0	12.7		26.2	35.6	3.3 ST R/Y	16	25.00
R80	ST	25.8	22.9	2.9	8.6	9.4	30.3	———		42.00
R45	ST	24.2	18.2	2.0	2.0		53.5	ST R/Y	16	20.50
R66	ST		47.1	52.9				———		30.00
R94	ST			25.3			45.8	28.9 ST R/G	21	15.00
R77	ST	29.6	3.3	0.5		5.6	2.2	58.7 ST R/G	20	30.00

TABLE 29--Continued

Percent of Time Spent in Males' Territories

Female	Species	PC B	PC R	PC A/R	F1	ST R/Y	ST Y/G	ST A/G With Mated	Date ^a	Sample Time (min.)
R38	3/4PC	37.4	10.4	52.2				PC A/R	10	20.50
R14	3/4PC						100.0	ST Y/G	10	0.67
W67	F1			42.8		57.1		ST R/Y	10	5.00
R55	F1	72.7	27.3					—		31.00
R74	F1		78.3	16.5		5.1		—		20.00
Y58	3/4ST		5.6	70.4	1.6	13.6	3.1	5.5 —		51.00
G58	3/4ST							100.0 ST R/G	10	0.50
B47	3/4ST	17.8	1.7	39.0	3.4	10.2	19.5	8.5 ST R/Y	16	25.00
R49	3/4ST	63.8				8.2	22.7	5.1 ST R/G	16	6.00

^aAll test dates in May 1978.

TABLE 30

AMOUNT OF TIME FEMALES SPENT IN MALE TERRITORIES

		Male Identification						
		PC B	PC R	PC A/R	F1	ST R/Y	ST Y/G	ST R/G
		Size of Territory (m ²)						
Percent		196.1 36.1	101.6 18.9	91.1 17.0	43.2 8.0	42.7 7.9	25.4 4.7	36.9 6.9
Time Spent by All Females (min.). Total Time = 484.25 min.								
Observed		134.0	79.0	106.2	10.0	41.0	74.3	39.6
Expected		174.9	90.6	81.5	38.3	37.9	22.5	33.1
$\chi^2 = 160.06$, df = 6, p 0.005								
Time Spent by Prairie Chicken Hens. Total Time = 46.33 min.								
Observed		33.3	11.8	1.2	0.0	0.0	0.0	0.2
Expected		16.9	8.7	7.9	3.7	3.7	2.2	3.2
$\chi^2 = 35.14$, df = 6, p 0.005								
Time Spent by Sharptail Hens. Total Time = 278.25 min.								
Observed		62.2	37.7	43.2	8.3	27.2	65.8	33.7
Expected		101.5	52.6	47.3	22.3	22.0	13.1	19.2
$\chi^2 = 252.72$, df = 6, p 0.005								
Time Spent by Hybrid Hens. Total Time = 159.67 min.								
Observed		38.4	29.5	61.7	1.6	13.8	8.4	5.7
Expected		30.2	58.3	27.1	11.0	12.8	12.6	7.5
$\chi^2 = 70.62$, df = 6, p 0.005								

($p < 0.005$, chi-square). Sharptail hens spent only 48.4% of their time in conspecific territories but this also was significantly greater than expected ($p < 0.005$). Three-quarter PC's were split with 1 hen spending all her time in sharptail, the other in prairie chicken territories. F1's spent 93% and 3/4 ST's 69.3% of their time in prairie chicken territories. None of the hybrid groups differed significantly from expected values.

Three prairie chicken and 7 sharptail hens copulated during the experiments, all with conspecifics. The remaining hens subsequently mated with conspecifics. All but 1 of the hybrid females that copulated did so with sharptails. Matings were bimodally distributed with peaks on 10 and 16 May. Prairie chicken, 3/4 PC and F1 females mated early while sharptails and most of the 3/4 ST's mated during the second peak.

Females, as a group, strongly preferred PC A/R's, ST Y/G's and ST R/G's territories and avoided those of PC R, PC B and the F1 (Table 30). Prairie chicken females remained in the territories of PC R and PC B more than expected and shunned those of PC A/R, sharptails and the F1. Sharptails preferred territories of PC B and sharptail males while avoiding PC R's and the F1's. Hybrid females occupied PC A/R's and PC B's territories more but PC R's, ST Y/G's and the hybrid's territories less than expected.

Male Aspects

Territorial boundaries were stable throughout the testing period and seemed to be determined by structures within the enclo-

TABLE 31
 PERCENT OF TIME SPENT BY PRAIRIE CHICKEN MALES
 IN SPECIFIED BEHAVIORS

Male	Relative ^a Mating Success	Boom	Behavioral Category					Time Sampled (min.)
			Whoop and/or Stamp	Neutral	Agonistic	Forward	Unidentified	
PC R	50	13.2	11.8	16.5	31.6	23.9	1.9	196.9
PC A/R	50	8.8	31.9	23.7	16.0	16.6	3.0	157.5
PC B	0	2.7	32.4	13.3	4.8	41.8	4.8	45.2

^aRelative Mating Success = Number of copulations by male
 x 100 divided by total number of copulations performed by species.

TABLE 32
 PERCENT OF TIME SPENT BY SHARPTAIL MALES
 IN SPECIFIED BEHAVIORS

Bird	Relative ^a Mating Success	Active Dancing	Quiet Dancing	Neutral	Agonistic	Unidentified	Time Sampled (min.)
ST R/Y	50	18.6	9.0	19.0	53.3	0.0	97.2
ST Y/G	8	30.3	16.1	30.7	20.6	2.3	189.6
ST R/G	42	40.7	38.8	6.6	12.2	1.7	152.7

^aRelative Mating Success = Number of copulations by male/
 total number of copulations by species x 100.

sure such as center posts or shelters. Non-territorial males frequently sought shelter when females were present, probably because of increased aggression by territorial males.

There was a significant difference among territorial prairie chicken males in the amount of time spent in different behaviors (G-Test, $p < 0.001$; Sokal and Rohlf, 1969) (Table 31). A posteriori comparisons (STP, Sokal and Rohlf, 1969) showed that each male differed significantly ($p < 0.001$) from the other 2. Based on the cumulative percent of epigamic (boom plus stamp and/or whoop) and agonistic (agonistic plus forward) behaviors, PC R was the most aggressive while PC A/R spent the most time in courtship. These males accounted for all of the matings made by prairie chicken males.

There were also significant differences among sharptail males ($p < 0.001$) and between each male ($p < 0.001$) (Table 32). ST R/G spent the greatest percent of time in courtship (active plus quiet dancing) while ST R/Y was the most aggressive of the 3. These males had considerably greater mating success than ST Y/G.

Discussion

Initial Female Preferences

Hens of both parental species showed strong initial preferences for conspecific males. This preference held for sharptails even though the south end of PC B's territory served as a refuge against overly anxious or aggressive males. This accounts for most of the time sharptail hens spent in prairie chicken territories. Hybrid hens did not show a clear initial preference for a particular species. Although

3/4 ST hybrids visited sharptail territories more than expected, the others were non-selective. All females, regardless of species, clearly avoided the F1's territory. This mimics the situation on natural display grounds where prairie chicken hens avoided an F1's central territory during 3 years of observations.

Initial preferences within a species may relate to male aggression. PC A/R appeared to repel hens because he frequently attacked them as they left the runway and entered his territory. Conversely, PC B was visited more than expected because he was not aggressive and allowed females to wander in the southern part of his territory. ST Y/G's territory also encompassed a small alcove in its northern extreme in which some sharptail hens could seek shelter. Hybrid hens strongly preferred PC A/R's territory, possibly because they were ambivalent and his territory allowed them access to both prairie chickens and sharptails. Thus, while territorial position may have influenced hybrid hens, it seemed unimportant to hens of either parental (P1) species except that peripheral territories provided resting areas.

Ultimate Preferences

Female prairie chickens and sharptails obviously favored conspecifics for all females of the parental species eventually mated with their own males. This preference is even more remarkable considering that birds were housed together. If imprinting was an important factor in species recognition, some females should have "mis-imprinted" and mated with a heterospecific. Although responses of hybrid hens were more ambiguous, most of the 3/4 ST's preferred sharptail males.

Apparently, species selection is strongly dominated by genetics in these species. This influence might have been predicted from the communal social system, rapid pair bond formation and mixed-species grounds. In sympatric areas, young birds may encounter males of both species on mixed grounds and errors in imprinting could occur, leading to more frequent hybridization unless there was a strong genetic component to species selection.

Factors Responsible for Mate Selection

Particular factors for species selection could not be determined from these experiments, but preliminary tests with paired stimulus trials indicated that vocalizations such as whoops and chिल्ks may be important. Other possible signals include size and color of cervical apteria, pinnae, elongated central rectrices and group synchronized dancing.

Some aspects of behavior may also be important in females selecting particular mates. The most successful males in this study were either the most aggressive (PC R, ST R/Y) or spent the most time in courtship (PC A/R, ST R/G). Further support for the behavioral hypothesis is that hybrid males, whose displays are frequently a blend of both parental species, appeared to repulse females in captivity and on naturally occurring display grounds. Oring (personal communication) has several years of data showing that central and peripheral males are quantitatively different in their displays when hens are present. Thus, behavior appears to be important in a general way but specific factors still need to be determined.

Possession of a territory was an essential factor in mating in that none of the hens showed any affinity for non-territorial males and never squatted in front of them. While territories on a communal display ground may not be essential in black grouse (Lyrurus tetrix) (Kruijt and Hogan, 1964, 1967), they seem to be a basic necessity for all North American communally displaying grouse (Scott, 1942; Lumsden, 1965; Robel, 1966, 1970; Wiley, 1973). Unfortunately, specific attributes of a territory that are important in mate choice could not be determined due to the small sample size.

Male prairie grouse do not defend any resource essential to females and the situation in species with leks is not comparable to that of other species with multi-purpose territories. Kruijt and Hogan (1967) suggested that female black grouse gravitate to the portions of leks with the highest density of males and Wiley (1973) had a similar explanation for preferences in sage grouse hens. However, most researchers that have studied the mating habits of these species (e.g. Lumsden, 1965; Wiley, 1973, 1974; Robel and Ballard, 1974) have also stated that hens wander among territories and appear to evaluate males. Thus, it appears that both position of territory and male behaviors interact as factors that determine a female's preference.

Summary

Female prairie chickens, sharptails and hybrids were tested for their ability to select conspecific mates. Hens of both parental species showed strong initial and ultimate preferences for conspecifics,

despite being raised in contact with both species. Hybrid hens, however, showed no initial preferences and only 3/4 ST backcrosses clearly favored a species. Much of this species recognition seems to be inherited.

Although characteristics of territories could not be distinguished from male attributes as factors responsible for species or mate selection, it appears that the possession of a territory is a prerequisite for mating in prairie grouse males. Male behavior in general also may influence mate selection.

GENERAL DISCUSSION

Communicatory Isolation in Prairie Grouse

The introduction to this dissertation discussed 5 ways that communication may help maintain species integrity. These methods included similar agonistic signals, divergence in courtship displays, development of non-homologous behaviors, increased selectivity for conspecific signals and retention of similar structure but divergence in information content in homologous signals. The following discussion relates these mechanisms to the displays of prairie grouse.

The first method, similar agonistic displays, was very apparent. Forward displays, stand offs and face offs and the forward posture of booming and cooing displays were virtually identical between species as were their clusterings. Support for interspecific recognition of aggression includes appropriate responses by males to some heterospecific agonistic vocalizations and mutually exclusive territories. The only apparent exceptions were gobbles and cork notes and they fall into a different category.

Divergence in courtship behaviors was evident, particularly when stereotyped booming displays and dancing, chilks and whoops, nuptial bows and specific aspects of flutter jumping are compared. These differences apparently were important to reproductive isolation for females tended to avoid heterospecifics and hybrids.

Both species had a few non-homologous signals including wing extension, cork notes, gobbles and pinnae elevation. These

may disrupt communication in both agonistic and courtship contexts. Prairie chicken pinnae elevation and sharptail wing extension and cork notes may be particularly important in communication between sexes. Male prairie chickens, however, were not confused by cork notes or gobbles for they reacted aggressively towards both.

Increased selectivity of sharptail males towards conspecific stimuli supports the fourth method of communicatory isolation. Females may have been as selective, but their perception of specific characteristics (e.g. sound frequencies or color vision) must be determined before any definitive statement can be made.

Whines of both species and booms and coos best exemplify homologous signals with different meanings. In prairie chickens, whines denoted several things including an ambivalence between staying and flying, aggression, potential danger and excitement. However, they only conveyed aggression and a high likelihood of remaining in sharptails. Similarly, booms functioned as long range advertisement, short range courtship and maintenance of status quo but coos were not involved in courtship.

Phylogenetic and Taxonomic Status

Based primarily on morphological characteristics, Short (1967) concluded that greater prairie chickens and sharp-tailed grouse were congeneric. This study showed that behaviors of both species are very similar. Although some of this similarity may be due to convergence caused by similar habitats and social systems, the 2 species have more homologous displays than either has with other species of

grouse. In view of this evidence plus hybrid fertility and naturally occurring backcrossing, I support the suggestion that the 2 species are congeners under Tympanuchus.

CONCLUSIONS

1. Greater prairie chickens and sharp-tailed grouse occupy a narrow and spotty zone of sympatry in north central and mid-western United States.
2. Hybridization occurs throughout this zone of sympatry at a rate of 1-3%. Within the Minnesota area, it ranged from 1.4-4.5% of prairie chicken males and 3.6-20% of sharptails. Evidence for backcrossing occurred in 1976 and 1978.
3. Hybridization is most likely to occur when one species is abundant, the other uncommon but not rare. Females of the least dense species are most likely to mate interspecifically due to difficulty in locating conspecifics.
4. Geographical isolation is an important factor in maintaining species integrity but is less important for prairie chickens than for sharptails because more of the former's range is in sympatry.
5. Seasonal, temporal and post-mating isolating mechanisms and habitat preferences are ineffective in maintaining species integrity.
6. The possibility of hybrid swarming may increase with land-use practices which result in island populations.
7. Many prairie grouse displays including booms, whines, coos, and wing (and associated displays) were polyvalent.

8. The greatest amount of divergence between species is in epigamic displays. Agonistic behaviors such as forward displays, face offs, cackles and whines are similar and permit interspecific communication. Playback experiments of cackles and existence of exclusive territories on mixed display grounds support these findings.
9. Displays of hybrids tend to be intermediate in form but retain similar functions as parental species' homologs.
10. Prairie grouse displays lack the temporal stereotypy seen in sage grouse but contain other forms of stereotypy which maximize transmission of signals through a noisy medium.
11. Homologous displays in parental species and hybrids have similar temporal, seasonal and interbehavioral relationships. Exceptions include whines and cackles.
12. Sharptails respond more vigorously to intraspecific and less strongly to interspecific stimuli than prairie chickens. The differences may be due to greater historical contact between sharptails and confamilials resulting in increased selectivity for conspecific stimuli.
13. Female prairie grouse readily select conspecifics for mates, even under captive conditions. Choice of mate appears to be influenced by the possession of a territory and by behavioral attributes of males.
14. Common cultural mechanisms are the most important factors maintaining species integrity in the zone of sympatry.

15. Based on similarities in displays, hybrid fertility and naturally occurring backcrosses, greater prairie chickens and sharp-tailed grouse should be congeneric under Tympanuchus.

APPENDICES

APPENDIX I

Questionnaire and Summary of Results

GREATER PRAIRIE CHICKEN AND SHARP-TAILED GROUSE
QUESTIONNAIRE

State or Province: _____

Name and Position of Respondee: _____

Date of Response: _____

1. Which of the species currently breeds in your state/province:

____ Greater Prairie Chicken ____ Sharptails ____ Both

____ Neither

2. What is the present estimated population size of each species?

____ Prairie Chickens

____ Sharptails

3. What is/was the maximum population size of each species?

____ Prairie Chickens

____ Sharptails

4. When were the species at their maximum numbers (years)?

____ Prairie Chickens

____ Sharptails

5. The population estimates above include:

____ Reproductive males only

____ Male and females

____ Other (please specify and include indices used).

6. What is the earliest known date of Greater Prairie Chickens breed-

QUESTIONNAIRE - Continued

ing in your state/province?

- ☐ Pre-settlement by white settlers
- ☐ 0-50 years after white settlement
- ☐ More than 50 years after white settlement

7. What is the earliest known date of sharptail grouse breeding in your state/province?

- ☐ Pre-settlement by white settlers
- ☐ 0-50 years after white settlement
- ☐ More than 50 years after white settlement

8. In general, what is the current status of Prairie Chickens in your state/province?

- ☐ Increasing
- ☐ Decreasing
- ☐ Stable
- ☐ Non-existent

9. In general, what is the current status of Sharptails in your state/province?

- ☐ Increasing
- ☐ Decreasing
- ☐ Stable

QUESTIONNAIRE - Continued

☐ Non-existent

10. Have Prairie Chicken x Sharptail hybrids ever been reported from your state/province?

☐ Yes

☐ No

11. Are hybrids currently found in your state/province?

☐ Yes

☐ No

12. Is there any indication that hybrids interbreed (i.e. hybrid x hybrid) in your state/province?

☐ Yes (please specify evidence) _____

☐ No

☐ Not known

13. Is there any evidence that hybrids backcross with either species of grouse in your state/province?

☐ Yes (please specify evidence) _____

☐ No

☐ Not known

14. Approximately what percentage of the grouse in your state/province are hybrids?

☐ Less than 1%

QUESTIONNAIRE - Continued

____ Between 1% and 10%

____ Between 10% and 15%

____ Greater than 15%

15. Do you feel that hybridization is a threat to the existence of either species of grouse in your state/province? (If so, which species?)

____ Yes

____ No

16. Please indicate the present distribution of Prairie Chickens and Sharptail grouse on the map provided.

17. Additional comments:

Thank you very much for your cooperation.

TABLE 33
RESULTS OF QUESTIONNAIRE ON
STATUS OF PRAIRIE GROUSE

State	Current Numbers or Date of Extinction ^a		Peak Years ^b		Current Status ^c		Hybrid ^d
	PC	ST	PC	ST	PC	ST	
Alaska	ne	va		2	4	1	0
Colorado	f	f	2; 1900	2; 1900	2	2	0
Idaho	ne	?		2; 1880	4	3	0
Illinois	r	ne	1; 1860	?; 1840	2	4	0
Indiana	1972	ne	1; 1870		4	4	0
Iowa	1950's	ne	1		4	4	0
Kansas	va	ne	1; ?		3	4	0
Kentucky	1930's	ne	2; 1810		4	4	0
Michigan	r	f	2; 1930	2; 1940	2	2	1, 1, No
Minnesota	f	va	1; 1870	2; 1910	2	2	3, 1, No
Missouri	a	ne	1; ?		3	4	0

TABLE 33--Continued

State	Current Numbers or Date of Extinction ^a		Peak Years ^b		Current Status ^c		
	PC	ST	PC	ST	PC	ST	Hybrid ^c
Montana	ne	a?		1; ?	4	3	0
Nebraska	r	a	2; 1880	1; ?	3	3	2, 2, No
New Mexico	ne	ne		2; 1900	4	4	0
North Dakota	r	va	2; 1910	1; 1870	2	3	2, 1, No
Ohio	1900	ne	1; ?		4	4	0
Oklahoma	va	ne	2; 1910		3	4	0
Oregon	ne	1950's		1; 1870	4	4	0
South Dakota	f	f	2; 1880	2; 1880	2	2	2, 1, No
Texas	f	ne	1; 1880		3	4	0
Utah	ne	va		1; ?	4	3	0
Washington	ne	a?		2; 1875		2	0
Wisconsin	f	f	1; 1880	1; 1885	3	2	3, 1, No
Wyoming	r?	a?	?	?	4	1	0

TABLE 33--Continued

Province	Current Numbers or ^a Date of Extinction		Peak Years ^b		Current Status ^c		
	PC	ST	PC	ST	PC	ST	Hybrid ^d
Manitoba	1950's	va	2; ?	1; ?	4	1	0
Ontario	1960's	a	1950	1968	4	3	3, 4, No

^aCurrent numbers: ne-- non-existent; r--rare; f--frequent; a--abundant; va--very abundant; date-- date of extinction.

^bPeak years: 1--pre-settlement; 2--0 to 50 years after settlement; approximate date.

^cCurrent status: 1--increasing; 2--decreasing; 3--stable; 4--non-existent.

^dHybrid: First number-- 0, no hybrids; 1--hybrids found in past; 2--hybrids currently found, no evidence of inbreeding; 3--evidence of current inbreeding. Second number-- percentage of grouse that are hybrids; 1--less than one percent; 2--one to ten percent; 3--ten to fifteen percent; 4--greater than fifteen percent. Yes or no--response to question concerning threat of hybridization.

APPENDIX II

Transition Matrices of Prairie Chicken,
Sharptail and Hybrid Activities

TABLE 34
TRANSITION MATRIX OF PRAIRIE CHICKEN ACTIVITIES

Preceding Behavior	Following Behavior	Face Off	Forward	Forward Rush	Run Parallel	Fight	Whine	Cackle	Boom	Stamp
Face Off		0	0	2	3	11	79	0	5	7
Forward		2	4	6	7	3	8	1	23	13
Forward Rush		12	8	6	8	4	18	2	30	25
Run Parallel		8	3	3	4	5	11	1	24	4
Fight		7	1	2	1	1	48	4	4	2
Whine		54	12	18	14	25	3368	516	92	154
Cackle		3	3	1	1	4	537	1	19	86
Boom		15	38	73	27	11	174	46	648	1235
Stamp		1	3	2	1	0	0	0	1931	23
Whoop		4	4	9	6	1	19	0	49	380
Stand Off		12	2	3	14	11	83	4	24	14
Walk		2	13	10	3	0	11	3	39	8
Comfort		0	7	7	2	1	30	8	56	22
Alert		0	0	1	0	0	4	3	9	7
Flutter Jump		0	0	3	0	0	36	152	2	15
Totals		120	98	147	91	77	4426	741	2955	1995

TABLE 34--Continued

Preceding Behavior	Following Behavior	Whoop	Stand Off	Walk	Comfort	Alert	Flutter Jump	Totals
Face Off		0	16	3	5	0	0	131
Forward		4	9	11	3	0	1	91
Forward Rush		7	24	3	2	1	0	144
Run Parallel		9	13	3	3	0	0	87
Fight		0	3	3	0	0	0	75
Whine		30	61	23	42	3	18	1062
Cackle		16	4	4	18	5	16	717
Boom		330	39	43	51	11	157	2250
Stamp		85	0	0	1	0	1	2050
Whoop		321	6	2	2	0	13	495
Stand Off		5	1	9	7	0	0	189
Walk		1	7	1	74	6	0	177
Comfort		3	1	68	10	26	2	233
Alert		2	0	7	17	0	1	51
Flutter Jump		1	0	0	0	0	6	209
Totals		814	184	180	235	52	215	12,363

TABLE 35

TRANSITION MATRIX OF SHARPTAIL ACTIVITIES

Preceeding Behavior	Following Behavior	Face Off	Forward Rush	Forward	Run Parallel	Stand Off	Fight	Whine	Cackle	Flutter Jump	Dance
Face Off		2	13	0	9	49	23	65	25	0	44
Forward Rush		44	6	0	12	7	0	1	1	0	15
Forward		0	1	0	0	0	0	0	1	2	0
Run Parallel		47	5	0	0	6	0	1	1	0	6
Stand Off		31	5	0	8	0	2	7	0	0	5
Fight		6	0	0	0	1	3	14	11	0	1
Whine		32	3	0	2	10	7	353	23	0	12
Cackle		17	0	0	2	1	4	17	10	0	0
Flutter Jump		0	3	0	0	0	0	0	0	0	17
Dance		18	15	0	4	4	0	2	0	4	38
Chilk		30	8	1	9	4	0	3	1	9	157
Gobble		31	9	0	12	1	2	9	1	0	26
Cork Notes		17	14	0	5	4	0	3	1	7	113
Coo		6	5	1	5	1	0	0	0	4	26
Walk		5	13	0	6	1	0	1	0	0	5
Comfort		11	11	4	2	5	0	3	0	0	7
Cluck		1	1	0	0	0	0	1	0	2	2
Alert		2	0	0	2	0	0	1	0	2	3
Totals		300	112	6	80	94	41	481	74	29	477

TABLE 35 --Continued

Preceding Behavior	Following Behavior	Chilks	Gobbles	Cork Notes	Coo	Walk	Comfort	Cluck	Alert	Totals
Face Off		12	26	0	20	23	23	2	6	342
Forward Rush		0	12	1	5	2	5	0	0	111
Forward		0	0	0	0	2	2	0	0	8
Run Parallel		1	7	0	2	0	4	2	2	84
Stand Off		5	5	0	2	8	14	2	2	96
Fight		0	0	0	0	1	0	1	0	38
Whine		3	11	0	1	2	9	0	1	469
Cackle		9	7	0	1	0	0	0	0	68
Flutter Jump		5	1	0	2	0	0	1	0	29
Dance		107	12	294	13	0	3	1	0	515
Chilk		948	10	34	20	0	4	3	2	1243
Gobble		5	613	1	245	18	31	7	4	1015
Cork Notes		136	13	655	12	0	3	0	0	983
Coo		9	235	16	1372	9	22	1	4	1716
Walk		0	29	0	8	0	43	7	5	123
Comfort		3	32	0	32	58	18	27	24	237
Cluck		4	13	0	2	11	14	80	0	131
Alert		3	1	0	1	7	22	3	0	47
Totals		1250	1027	1001	1738	141	217	137	50	7255

TABLE 36
TRANSITION MATRIX OF HYBRID ACTIVITIES

Preceding Behavior	Following Behavior	Face Off	Forward Rush	Forward	Stand Off	Fight	Run Parallel	Gobble	Coom	Stamp
Face Off		1	2	0	11	6	4	3	0	4
Forward Rush		17	8	1	7	2	7	3	6	7
Forward		0	0	0	0	0	0	1	1	1
Stand Off		7	1	1	0	0	2	2	1	1
Fight		7	0	0	1	0	0	0	0	0
Run Parallel		12	2	0	2	1	1	5	5	2
Gobble		9	1	1	2	1	2	13	7	2
Coom		1	27	2	2	0	4	12	17	75
Stamp		0	2	0	0	0	0	2	171	5
Whoop		2	10	0	1	0	2	0	7	55
Whine		20	8	1	5	16	8	5	0	8
Cackle		2	3	0	1	0	1	0	0	16
Flutter Jump		0	0	0	0	0	0	0	0	1
Comfort		2	5	0	0	1	3	0	3	2
Walk		0	9	0	0	1	2	3	0	0
Totals		80	78	6	32	28	36	49	218	180

TABLE 36 --Continued

Preceding Behavior	Following Behavior	Whoop	Whine	Cackle	Flutter Jump	Comfort	Walk	Totals
Face Grf		5	36	1	0	7	3	83
Forward Rush		8	8	0	0	2	3	79
Forward		0	1	0	1	0	1	6
Stand Off		1	10	2	0	1	2	31
Fight		0	15	2	0	0	0	25
Run Parallel		2	3	0	0	0	1	36
Gobble		3	4	0	1	1	1	48
Coom		45	8	7	7	2	3	212
Stamp		6	0	1	0	0	1	188
Whoop		110	4	1	1	1	0	194
Whine		5	595	22	0	2	3	678
Cackle		5	18	1	1	2	1	51
Flutter Jump		1	0	9	0	0	1	12
Comfort		1	0	1	0	2	7	28
Walk		0	0	0	0	0	0	15
Totals		193	683	49	11	34	27	1694

APPENDIX III

Correlation Matrices of Prairie Chicken,
Sharptail and Hybrid Activities

TABLE 37

CORRELATION MATRIX OF PRAIRIE CHICKEN ACTIVITIES

Behavior	Face Off	Forward	Forward Rush	Run Parallel	Fight	Whine	Cackle	Boom	Stamp	Whoop	Stand Off
Face Off	1.000										
Forward	0.324	1.000									
Forward Rush	0.318	0.970	1.000								
Run Parallel	0.550	0.827	0.866	1.000							
Fight	0.957	0.322	0.355	0.629	1.000						
Whine	0.109	0.136	0.138	0.092	0.270	1.000					
Cackle	0.879	0.161	0.158	0.275	0.743	0.222	1.000				
Boom	-0.114	-0.051	-0.157	-0.194	-0.186	-0.147	-0.080	1.000			
Stamp	0.189	0.883	0.957	0.797	0.241	0.207	0.054	0.503	1.000		
Whoop	0.160	0.884	0.941	0.760	0.222	0.187	0.024	0.946	0.999	1.000	
Stand Off	0.930	0.599	0.604	0.792	0.930	0.103	0.740	-0.167	0.456	0.425	1.000
Walk	0.148	0.566	0.509	0.385	0.171	0.113	0.130	-0.143	0.395	0.391	0.255
Comfort	0.330	0.686	0.550	0.411	0.271	0.152	0.300	-0.149	0.403	0.397	0.445
Alert	-0.089	0.399	0.322	0.108	-0.091	0.114	-0.030	-0.114	0.238	0.238	-0.005
Flutter Jump	0.203	0.917	0.977	0.807	0.282	0.281	0.107	-0.106	0.974	0.965	0.481

TABLE 37--Continued

Behavior	Walk	Comfort	Alert	Flutter Jump
Walk	1.000			
Comfort	0.911	1.000		
Alert	0.944	0.819	1.000	
Flutter Jump	0.438	0.455	0.283	1.000

TABLE 38

CORRELATION MATRIX OF SHARPTAIL ACTIVITIES

Behavior	Face Off	Forward	Forward Rush	Run Parallel	Stand Off	Fight	Whine	Cackle	Flutter Jump	Dance	Chilk
Face Off	1.000										
Forward	0.233	1.000									
Forward Rush	-0.134	0.214	1.000								
Run Parallel	0.764	0.560	-0.115	1.000							
Stand Off	0.759	0.382	-0.056	0.351	1.000						
Fight	0.303	0.208	-0.159	0.227	0.949	1.000					
Whine	0.107	0.221	-0.134	0.243	0.920	0.995	1.000				
Cackle	0.194	0.019	-0.181	0.004	0.757	0.880	0.963	1.000			
Flutter Jump	-0.076	0.288	0.057	0.076	-0.173	-0.280	-0.255	-0.286	1.000		
Dance	0.208	0.488	0.068	0.378	0.143	0.029	0.058	-0.011	0.889	1.000	
Chilk	0.009	0.595	-0.119	0.025	-0.005	-0.103	-0.070	-0.127	0.833	0.929	1.000
Gobble	-0.174	0.076	0.250	0.109	-0.029	-0.044	-0.066	-0.093	0.188	0.017	-0.050
Cork Notes	-0.023	0.495	-0.071	-0.008	-0.047	-0.128	-0.113	-0.146	0.394	0.903	0.992
Coo	0.220	0.214	0.043	0.485	-0.117	-0.052	-0.012	-0.138	-0.087	0.060	-0.043
Walk	-0.129	0.330	0.839	0.037	0.221	0.159	0.186	0.018	-0.281	-0.161	-0.209
Comfort	-0.144	0.334	0.021	0.377	0.165	0.190	0.160	0.021	-0.244	-0.161	-0.263
Cluck	-0.158	0.323	0.891	-0.048	-0.039	-0.109	-0.071	-0.180	-0.175	-0.102	-0.168
Alert	-0.116	0.358	0.916	0.025	0.165	0.078	0.100	-0.012	-0.192	-0.082	-0.182

TABLE 38 --Continued

Behavior	Gobble	Cork Notes	Coo	Walk	Comfort	Cluck	Alert
Gobble	1.000						
Cork Notes	-0.016	1.000					
Coo	0.597	-0.033	1.000				
Walk	0.151	-0.172	0.272	1.000			
Comfort	0.352	-0.202	0.415	0.906	1.000		
Cluck	0.036	-0.105	0.257	0.946	0.831	1.000	
Alert	0.177	-0.142	0.162	0.966	0.861	0.964	1.000

TABLE 39
CORRELATION MATRIX OF HYBRID ACTIVITIES

Behavior	Face Off	Forward Rush	Forward	Stand Off	Fight	Run Parallel	Gobble	Boom	Stamp	Whoop	Whine
Face Off	1.000										
Forward Rush	-0.114	1.000									
Forward	0.347	0.648	1.000								
Stand Off	0.884	0.008	0.221	1.000							
Fight	0.705	0.043	0.172	0.540	1.000						
Run Parallel	0.802	0.463	0.541	0.673	0.735	1.000					
Gobble	0.213	0.793	0.785	0.252	0.209	0.501	1.000				
Boom	-0.249	-0.100	-0.176	-0.205	-0.162	-0.264	0.028	1.000			
Stamp	-0.256	0.868	0.468	-0.071	-0.161	0.142	0.561	0.435	1.000		
Whoop	-0.112	0.919	0.731	0.095	-0.072	0.287	0.866	0.370	0.987	1.000	
Whine	0.284	-0.076	-0.040	0.777	0.767	0.280	0.039	-0.243	-0.018	0.067	1.000
Cackle	0.398	0.278	0.326	0.113	0.786	0.503	0.301	-0.130	0.113	0.189	-0.097
Flutter Jump	-0.304	0.856	0.682	-0.120	-0.222	0.058	0.754	-0.174	0.834	0.947	-0.036
Comfort	0.092	0.209	-0.010	0.727	0.350	0.446	0.211	-0.244	0.021	0.127	0.703
Walk	0.127	0.263	0.202	0.246	0.256	0.524	0.198	-0.139	-0.062	0.174	0.043

TABLE 39--Continued

Behavior	Flutter			
	Cackle	Jump	Comfort	Walk
Cackle	1.000			
Flutter Jump	0.145	1.000		
Comfort	0.008	-0.014	1.000	
Walk	0.173	0.047	0.637	1.000

APPENDIX IV

Distance Matrices of Prairie Chicken,
Sharptail and Hybrid Activities

TABLE 40

DISTANCE MATRIX OF PRAIRIE CHICKEN ACTIVITIES

Behavior	Face Off	Forward	Forward Rush	Run Parallel	Fight	Whine	Cackle	Boom	Stamp	Whoop	Stand Off
Face Off	0.00										
Forward	14.26	0.00									
Forward Rush	19.50	10.07	0.00								
Run Parallel	11.89	5.65	13.38	0.00							
Fight	8.54	10.17	18.10	6.37	0.00						
Whine	156.83	157.11	155.31	157.89	157.70	0.00					
Cackle	135.26	146.42	144.42	145.64	142.95	59.24	0.00				
Boom	535.97	535.69	535.86	536.25	536.52	555.52	550.49	0.00			
Stamp	356.02	351.07	341.29	353.77	358.04	336.51	362.58	96.40	0.00		
Whoop	90.79	84.44	75.17	87.47	91.71	156.85	163.38	512.71	254.27	0.00	
Stand Off	8.27	15.45	16.14	14.71	14.35	154.59	133.38	536.11	349.35	84.88	0.00
Walk	22.59	17.58	19.22	19.29	20.95	156.37	144.09	536.20	349.78	85.11	22.75
Comfort	23.76	20.38	21.11	23.37	24.67	152.95	139.65	535.85	347.22	83.52	21.92
Alert	16.90	10.05	18.86	10.07	10.49	158.65	148.81	536.63	358.76	92.22	21.22
Flutter Jump	41.25	33.65	23.99	36.70	41.08	149.00	141.58	536.28	318.86	53.56	36.26

TABLE 40--Continued

	Walk	Comfort	Alert	Flutter Jump
Walk	0.00			
Comfort	7.86	0.00		
Alert	16.23	24.83	0.00	
Flutter Jump	37.10	36.96	41.55	0.00

TABLE 41

DISTANCE MATRIX OF SHARPTAIL ACTIVITIES

Behavior	Face Off	Forward Rush	Forward	Run Parallel	Stand Off	Fight	Whine	Cackle	Flutter Jump	Dance	Chilk
Face Off	0.00										
Forward Rush	17.09	0.00									
Forward	23.68	8.00	0.00								
Run Parallel	15.70	4.92	6.15	0.00							
Stand Off	19.10	10.77	12.83	10.89	0.00						
Fight	22.80	8.01	6.22	6.61	7.31	0.00					
Whine	19.98	15.35	17.44	15.39	7.15	11.30	0.00				
Cackle	21.71	9.81	9.00	8.99	7.77	4.10	10.45	0.00			
Flutter Jump	22.78	6.96	3.18	5.54	12.91	6.95	17.55	9.42	0.00		
Dance	43.30	46.14	50.69	47.35	43.06	49.88	48.88	49.62	47.92	0.00	
Chilk	42.25	38.51	43.55	41.93	43.10	43.49	44.67	43.69	41.51	13.44	0.00
Gobble	60.17	58.12	60.21	58.65	59.80	60.16	60.84	60.25	59.83	69.49	69.58
Cork Notes	72.33	70.37	74.06	73.01	74.09	74.35	75.55	74.61	72.83	34.07	47.01
Coo	57.03	59.40	62.05	58.94	62.77	61.93	62.02	62.47	61.94	70.63	71.99
Walk	24.67	13.77	15.71	16.48	15.73	19.09	16.84	16.66	51.02	45.68	57.30
Comfort	22.20	13.31	17.33	13.64	16.73	16.00	18.83	16.73	16.90	49.00	44.75
Cluck	23.04	7.53	6.38	7.83	13.66	9.12	17.83	11.17	7.67	50.19	43.76
Alert	23.03	7.13	5.55	7.14	12.34	7.77	16.78	10.00	6.97	50.10	43.74

TABLE 41--Continued

Behavior	Gobble	Cork Notes	Coo	Walk	Comfort	Cluck	Alert
Gobble	0.00						
Cork Notes	90.53	0.00					
Coo	9.55	93.48	0.00				
Walk	57.30	75.80	57.78	0.00			
Comfort	53.87	74.95	55.17	6.75	0.00		
Cluck	59.45	74.11	59.83	9.81	14.58	0.00	
Alert	58.78	74.27	60.64	10.42	14.25	1.82	0.00

TABLE 42
DISTANCE MATRIX OF HYBRID ACTIVITIES

Behavior	Face Off	Forward Rush	Forward	Stand Off	Fight	Run Parallel	Gobble	Coom	Stamp	Whoop	Whine
Face Off	0.00										
Forward Rush	9.72	0.00									
Forward	8.43	8.32	0.00								
Stand Off	6.30	8.38	3.73	0.00							
Fight	6.11	8.79	4.55	3.73	0.00						
Run Parallel	5.42	7.12	3.10	2.43	3.07	0.00					
Gobble	7.29	5.66	3.59	3.98	4.84	2.91	0.00				
Coom	47.98	47.05	47.54	47.61	47.76	47.54	46.96	0.00			
Stamp	26.26	18.75	25.90	25.62	26.32	24.93	23.68	14.37	0.00		
Whoop	13.90	5.86	12.44	12.22	13.16	11.61	9.51	45.86	8.92	0.00	
Whine	6.63	13.00	12.54	9.46	10.58	11.22	11.69	48.99	25.47	14.80	0.00
Cackle	7.27	8.05	6.57	6.58	3.96	5.23	5.87	47.73	24.61	12.16	11.24
Flutter Jump	8.94	7.17	1.52	4.18	5.20	3.49	2.93	47.54	24.66	11.17	12.41
Comfort	8.13	7.85	2.35	2.37	4.09	2.51	3.54	47.58	25.60	12.28	10.81
Walk	7.75	7.42	2.35	3.29	4.22	2.27	3.43	47.27	25.59	12.02	11.71

TABLE 42--Continued

Behavior	Flutter			
	Cackle	Jump	Comfort	Walk
Cackle	0.00			
Flutter Jump	6.21	0.00		
Comfort	6.57	2.79	0.00	
Walk	6.12	2.76	1.41	0.00

APPENDIX V

Activity Indices of Prairie Chickens and Sharptails

TABLE 43
INDEX OF PRAIRIE CHICKEN ACTIVITIES

Rate of Booms	
0	$0 \leq N \leq 2.0$ booms per minute
1	$2.0 < N \leq 6.3$ b.p.m.
2	$N > 6.3$ b.p.m.
Rate of Whines	
0	$0 \leq N \leq 4.1$ whines per minute
1	$4.1 < N \leq 12.5$ w.p.m.
2	$N > 12.5$ w.p.m.
Agonistic Behavior (total of face offs, fights, forward rushing and running parallel)	
0	$0 \leq N \leq 0.5$ acts per minute
1	$0.5 < N \leq 1.6$ a.p.m.
2	$N > 1.6$ a.p.m.
Minimum Distance From Speaker	
0	Distance greater than 10m
1	Distance between 3m and 10m
2	Distance less than 3m
Orientation Towards Speaker	
0	No apparent orientation
1	Looks towards speaker
2	Approaches speaker
Alertness	
0	No alert responses
1	Semi-alert posture
2	Upright alert posture

TABLE 43 -- Continued

Courtship Behavior	
0	No courtship behavior
1	N \geq 5 stamping bouts per minute
2	Frequent whoops and stamping

TABLE 44
INDEX OF SHARPTAIL ACTIVITIES

Rate of Coos	
0	$0 \leq N \leq 1.3$ coos per minute
1	$1.3 < N \leq 3.7$ c.p.m.
2	$N > 3.7$ c.p.m.
Rate of Gobbles	
0	$0 \leq N \leq 1.0$ gobbles per minute
1	$1.0 < N \leq 3.0$ g.p.m.
2	$N > 3.0$ g.p.m.
Agonistic Behavior (total of face offs, fights, forward rushes and running parallels)	
0	$0 \leq N \leq 0.6$ acts per minute
1	$0.6 < N \leq 1.7$ a.p.m.
2	$N > 1.7$ a.p.m.
Minimum Distance From Speaker	
0	Distance greater than 10m
1	Distance between 3m and 10m
2	Distance less than 3m
Orientation Towards Speaker	
0	No apparent orientation
1	Looks towards speaker
2	Approaches speaker
Alertness	
0	No alert behavior
1	Semi-alert posture
2	Upright alert

TABLE 44--Continued

Courtship Behavior	
0	No courtship behavior
1	More than 3 dances per minute
2	Frequent dances plus chilks or cork notes

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