

CHARACTERIZING THE FUNCTIONS OF COYOTE VOCALIZATIONS
THROUGH THE USE OF PLAYBACK

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THESIS

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THROUGH THE USE OF PLAYBACK

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Abstract: We examined the functions of three vocalizations in a free-ranging coyote (*Canis latrans*) population on the Arid Lands Ecology Reserve, in south-central Washington. Between September 1987 and August 1988, playbacks (i.e., lone howls, group howls, and group yip-howls) were broadcast to radio-collared coyotes in 10 territories.

Our major objective was to investigate behavioural responses, both vocal reply and movement, to vocal stimuli. More specifically, we examined the following: the seasonality of response, coyote response to vocalization type, the effect of environmental factors on response, and the role of vocalizations in territorial maintenance.

Coyotes responded to group vocalization playback, including group howls and group yip-howls, more often during breeding season and early denning season. During breeding season, coyotes were more likely to vocalize in groups, respond with both movement and vocalization, and move to group yip-howl more than

group howl playbacks. During early denning season, elicited vocalizations peaked. However, after whelping (April and May) coyote vocalization rates gradually declined. Elicited movement rates remained high during denning season, peaking in May. Coyotes vocalized and moved less in response to playbacks during pup-rearing season, but vocalized more to group yip-howl than to group howl playbacks; moreover, they moved more in response to lone howl than to group vocalization playbacks. Finally, during dispersal period, both movement and vocalizations oscillated between high and low response rates.

Coyotes appeared to move more in response to playback during moderate winds (8-16 km/hr). Other environmental factors, however, did not significantly affect response to playbacks.

Finally, coyotes vocalized more and moved significantly more to playbacks broadcast within core territories, than to those broadcast along boundaries or outside territories. Regardless of playback location or playback type, coyotes commonly approached the stimulus site (42.5% of all elicited movement).

In conclusion, coyotes on the Arid Lands Ecology Reserve exhibited a seasonal response to vocal stimuli, differentiating between playback type. Additionally, they appeared to retain knowledge of spatial relationships, responding more often to playbacks broadcast within their territories. Hence, coyotes may respond to and emit vocalizations (primarily group vocalizations) as a form of passive, territory-dependent avoidance. Primarily during breeding and early denning seasons, inter-territory vocalizing may serve a crucial role in spacing

densely-packed groups within an area of limited resources.
However, intra-territory vocalizing may gain importance during
pup-rearing season, as social bonds are reaffirmed.

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PREFACE

This thesis is written as a manuscript which will be submitted to a professional journal. Accordingly, the writing format adheres to the guidelines of Animal Behaviour. Because this research was conducted with several colleagues, the personal pronoun "we" is used and the manuscript will be submitted with multiple authorship.

INTRODUCTION

Management of the coyote (*Canis latrans*) remains one of wildlife biology's principal challenges (Lehner 1976). The coyote has been extensively controlled for over a century (Young and Jackson 1951); however, its extreme adaptability has often rendered predator-control efforts ineffectual. The coyote's ability to adapt to a changing environment is ultimately a consequence of its complex behaviour, especially its manifold communication system (Lehner 1978a).

Howling, a form of canid auditory communication, represents one of the few long-distance, audible signals emitted by terrestrial mammals (Nikol'skii et al. 1986). Specifically, vocalizations are the prominent form of auditory communication in the coyote (Lehner 1978a). Although considered the most vocal of all North American wild mammals (Gier 1975), due to their secretive nature free-ranging coyotes are particularly difficult to observe directly. However, in investigating coyote vocalizations, researchers may indirectly gain knowledge concerning their behavioural ecology.

Several long-term studies have provided important insight into canid behavior and communication. Vocalization studies have been conducted on coyotes, red fox (*Vulpes vulpes*), domestic dogs (*Canis familiaris*), and wolves (*Canis lupis*). Wolf communication has been most intensively

studied, including howling as a means of communication (Theberge and Falls 1967), howling as a form of territorial maintenance and spacing (Harrington and Mech 1979; 1983, respectively), howling response as a censusing technique (Pimlott 1960; Harrington and Mech 1982), wolf discrimination between pup and adult howls (Harrington 1986), and the spatial-temporal features of howling (Nikol'skii et al. 1986).

Coyote research, especially studies investigating behavioural ecology, has proliferated in the past 15 years (e.g., Bekoff 1978; Bowen 1978; Camenzind 1978; Bekoff & Wells 1980; Andelt 1985). Early vocalization research focused on describing different types of coyote howls and hypothesizing their function. For example, McCarley (1975) spectrographically analysed and described long-distance vocalizations. Lehner (1978b) later presented a lexicon of 11 vocalizations and discussed their respective functions. Five vocalizations defined by Lehner (1978a; 1978b) were significant to this study because of their frequent use and behavioural context:

1. bark -- burst of high amplitude & short
 (B) duration. Used in threat or alarm.

2. bark-howl -- short howl interspersed with barks.
 (BH) Used in threat or alarm.

3. lone howl -- high amplitude; slight to moderate
(LH) frequency modulation; long duration.
Used when group members are separated
or when members are responding to
distant howling.
4. group howl -- same as lone howl but given by two or
(GH) more coyotes polyphonically or
antiphonally. Used when group members
are separated or when members are res-
ponding to distant howling. Possibly
represents a low-intensity territorial
announcement.
5. group yip-howl -- high amplitude; rapid yipping
(GYH) interspersed with howls of generally
shorter duration than lone howl or
group howl. Used when group members
are reunited or when members are res-
ponding to distant howling. Possibly
represents a high-intensity territorial
announcement.

Lehner (1978a; 1978b) discussed the plausible functions of these vocalizations, although most were defined on the basis of contextual information (anecdotal observations). This research, which primarily defined howl types within

their behavioural context, laid an important foundation for further investigation.

Several studies have investigated temporal variation of spontaneous vocalizations (Laundre 1981; Walsh and Inglis 1989), and examined the feasibility of siren-censusing coyotes (Wolfe 1974; Wenger and Cringan 1978). Moreover, the functions of group howls and group yip-howls have been cursorily tested using playback (Lehner 1982). Finally, Barnum et al. (1987) tested the hypothesis that foreign scent-marking and excess howling suppresses reproduction in coyote populations: hand-reared coyotes subjected to repeated howling produced litters with higher male sex ratios, implying that coyotes may have behavioural-physiological feedback mechanisms (such as communal howling) that affect reproductive success (Clark 1972; Hornocker 1972; Camenzind 1974; Lehner 1976; Barnum et al. 1987).

To date, no research has investigated how coyotes move in response to howling stimuli, information potentially important in revealing the territorial function of vocalizations (Harrington and Mech 1979). For example, Lehner (1982) broadcast playbacks to a population of non-radio-collared coyotes whose social status and territorial boundaries were unknown; although several other studies examined vocalizations of radio-collared coyotes (e.g., Wenger and Cringan 1978; Laundre 1981), none monitored movement nor addressed territory locations.

The purpose of our research was to further investigate the behavioural functions, particularly the territorial function of different vocalizations, using radio-collared coyotes on the Arid Lands Ecology (ALE) Reserve, near Richland, Washington. The study's use of radio-collared animals was of primary importance for several reasons: 1) collared coyotes' movements had been monitored for several years, therefore we had knowledge of their territorial boundaries and social status (i.e. alpha female, associate male); 2) choice of playback sites were based on where radio-collared coyotes were located each night; and 3) we were able to monitor movement of all collared coyotes in the area before, during, and after each playback.

In general, coyotes are difficult to observe directly due to their furtive nature, their crepuscular and nocturnal activity, and their ability to range widely (Kleiman and Brady 1978). Hence, we indirectly observed behavioural responses through the use of vocal stimuli. Specifically, we investigated behavioural responses (vocal reply and movement) to playback stimuli in an attempt to address the following objectives: 1) to compare responses between and within seasons; 2) to compare responses to different types of vocalizations; 3) to better define key environmental factors influencing response; and 4) to scrutinize the role of coyote auditory signals in territorial maintenance (Appendix A).

Methods

Study Area

The study area lies in south-central Washington on the Department of Energy's Hanford ^{site} Reserve (Appendix B). In 1967, the Atomic Energy Commission set aside 307 km² within Hanford as an ecological area, now called the Arid Lands Ecology (ALE) Reserve (Thorp and Hinds 1977). The ALE Reserve is bordered by the Rattlesnake Hills to the south-southwest, and by Washington Highways 240 to the northeast, and 241 to the north.

Located in the northwest portion of the ALE Reserve, the study area covers approximately 154 km². Rattlesnake Mountain, the study area's prominent point, is 1060 meters high; its northeastern face drops steeply to 650 meters, then gradually slopes northward to 150 meters at Cold Creek Valley (Thorp and Hinds 1977).

The ALE Reserve lies in the rainshadow of the Cascade Mountains in one of the most arid regions of the Pacific Northwest (Stoel 1976). Summers are hot and arid (mean July maximum temperature of 33.3°C); winters are cool (mean January minimum temperature of -10.2°C). The annual precipitation, usually occurring during the late fall and winter months, averages 171.2 mm (Rickard 1972).

The entire ALE Reserve is classified as a semi-arid, shrub-steppe community and is located within the *Artemisia*

tridentata / *Agropyron spicatum* Zone, the most arid vegetation zone found in eastern Washington (Daubenmire 1970). Some major shrub-steppe communities found within the reserve include *Artemisia/Poa*, *Artemisia/Agropyron*, *Atriplex/Poa*, *Sarcobatus/Bromus-Distichlis*, *Eurotia/Poa*, *Eriogonum/Poa*, and *Salix/Populus*. These plant associations, actually a mosaic of disturbed and undisturbed communities (Rickard 1972), periodically experience wildfire; the last extensive fire occurred in August, 1984. Thus, ALE Reserve is a patchwork of grasslands and isolated shrubfields.

Unlike the more prevalent natural disturbance of fire, human disturbance on the ALE Reserve is minimal. Because public access has been restricted since World War II, disturbances have been limited to farming and grazing in 1943, and military maneuvers in 1965. However, heavy vehicle tracks still scar the landscape from this 1965 disturbance (Rickard 1972).

Although water is scarce on the study area, two permanent sources, located at Rattlesnake Springs and Snively Gulch, sustain riparian flora and fauna. Important riparian species include *Populus trichocarpa*, *Prunus americana*, and several *Salix* species. These springs provide crucial nesting habitat for birds and support numerous terrestrial and aquatic fauna (Rickard 1972).

Coyotes inhabiting the ALE Reserve have experienced no predator control since 1952 (Crabtree 1989). With the exception of research efforts, the ALE Reserve coyotes are

unexploited. In 1984, Crabtree (1989) initiated research on this population. After examining the population dynamics, food habits, and social structure of the coyotes, Crabtree (1989) reported that the population exhibited a healthy, breeding age-class of animals three years and older. In contrast, exploited populations commonly exhibit first year breeding age-classes (Crabtree 1989).

Between August 1987 and August 1988, 10 territorial coyotes inhabiting the study area wore functional radio-collars; we knew the approximate boundaries of nine territories. This situation, then, presented an opportunity to continue researching unanswered questions regarding coyote communication and territorial behavior.

Study Animals

During the three years previous to this study, 80 adult coyotes were captured with #3 offset jaw, leg-hold traps, and 27 adults (20 recaptures) were captured using a netgun from a helicopter (Crabtree 1989). We trapped an additional 6 coyotes in February 1988 using leg-hold traps and similar trapping methods as Crabtree (1989).

All captured coyotes were fitted with radio-collars, marked with colored ear flags and numbered ear tags, weighed, and sexed. We described individuals according to a condition index (overall estimate of the animal's health), and reproductive condition (description of genitalia and mammae). Additionally, we extracted one premolar from each

captured coyote; premolars were later analysed to determine age (Crabtree 1989).

Playbacks were broadcast to both radio-collared and non-radio-collared coyotes, at locations where approximate territorial boundaries were both known (approximately 30 locations) and unknown (approximately 8 locations).

Equipment and Procedures

Recording Sessions

Although we opportunistically recorded free-ranging coyotes throughout the year, we initially conducted sessions solely for recording local vocalizations. During September and October 1987, we taped spontaneous vocalizations (those vocalizations not artificially elicited) primarily at dusk and secondarily at dawn. Six to eight known territories' vocalizations were recorded on ALE; additionally, vocalizations were recorded at locations in the Hanford vicinity.

Spontaneous vocalizations took precedence during recording sessions. When a nearby group spontaneously vocalized, their howls were picked up through an omnidirectional microphone mounted on a 1 m parabolic dish, and recorded on a Uher 4000 field tape recorder (19 cm/s); the parabolic dish enhanced long-distance sound reception, therefore, under ideal conditions (low wind, and dense, cool air) we recorded coyotes howling within a one mile radius.

If no animals vocalized within a one-hour waiting period, we then broadcast a GYH playback; all elicited vocalizations were then recorded. No more than two playbacks were broadcast per night in one territory, nor were playbacks conducted if resident animals spontaneously vocalized. Additionally, we recorded all vocalizations elicited during standardized playback experiments conducted throughout the year. Field recordings were later edited, categorized according to territorial groups, and selectively used for playbacks.

Playback Sessions

We conducted playback experiments from September 1987 through August 1988, primarily between 1600 and 0900 hours. Approximately 18 sites were visited every 10 days. Playbacks were broadcast through a Uher 4000 tape recorder connected to a 12-volt powered amplifier, and a Realistic loudspeaker aimed skyward from the roof of a vehicle. Vocalizations played through this system were calibrated to sound authentic to a human listener stationed within a 1.6 km radius.

We conducted two principle types of playback experiments: paired group vocalization (GYH and GH) playbacks, and lone howl playbacks. We purposely paired group vocalization playbacks to minimize the variability in response levels (Harris et al. 1983), and to test Lehner's field experiment (1982) on a population with documented home

ranges. During a group vocalization playback session, study subjects heard numerous GYH and GH recordings randomly chosen from the following recording sites: foreign coyotes from Dubois, Idaho (three GYHs; two GHs); foreign coyotes inhabiting agricultural lands near the study area (two GYHs; two GHs); and neighbour and non-neighbour vocalizations taken directly off the reserve (seven GYHs; five GHs). We strived to broadcast a variety of playback stimuli, thereby sampling the population of vocalization stimuli as well as that of the study animals (Kroodsma 1989).

Unlike the GYH and GH recordings, all lone howl recordings were procured exclusively on the ALE Reserve. Lone howl playbacks were broadcast between 15 April and 15 August 1989. These recordings were not paired with other playbacks. During a lone howl playback session, we broadcast any one of 13 recordings to radio-collared animals (two 5 s recordings of 2 howls each, broadcast within a 5 s interval). We monitored vocal response and movement using the same methods as those of group vocalization playbacks.

Based on recording site, lone howl, group howl, and group yip-howl recordings were further categorized as follows:

neighbour -- vocalizations recorded from a territorial group were played to an adjacent territorial group.

- non-neighbour -- vocalizations recorded from a territorial group were played back to a territorial group that is separated from the other by at least one intervening territory (Raemaekers & Raemaekers 1986).
- foreign -- vocalizations recorded off ALE (Badger Canyon, WA, or Dubois, ID) were played to territorial groups on ALE.

Finally, we randomly broadcast noise playbacks consisting of alarms, telephone rings and grinding sounds (wide-frequency tones representative of a neutral sound) during July and August 1989. Noise playbacks were broadcast for 40 s, approximating the length of group vocalization (GYH and CH) playbacks.

We evaluated two types of behavioural responses to playbacks during all sessions: vocal reply to stimulus, and movement of radio-collared coyotes before, during, and after playbacks. Six major characteristics were recorded regarding vocal response, including: vocal response type (lone howl, group howl, group yip-howl, bark, and bark howl), response latency (number of seconds until vocal reply), bout duration, direction and approximate distance of

vocalizations from stimulus, and the approximate number of vocalizing individuals and groups.

Coyote movement was monitored through the use of radio-telemetry. Prior to each playback session, radio-collared coyotes' locations were plotted on 15 minute topographic maps after two separate relocations were taken; the pre-playback location was then calculated as a triangulation of these two azimuths (ideally these lay at a 45° angle from one another). Although we monitored coyote movement throughout the playback session, only relative movement patterns were recorded because we were unable to triangulate locations after initially locating coyotes. Therefore, movement behaviour was categorized as toward, away from, downwind from, or no movement relative to the playback site; we assumed no movement reflected no response to playback.

Playback locations varied with the radio-collared coyotes' proximity to respective territorial boundaries (Fig. 1). Boundary locations were based on three years of fixed-station tracking; home ranges were generated for eight alpha animals of different territories by calculating the area inside a 0.001 probability contour of a utilization distribution (the animal's space-use) (Crabtree 1989). We attempted to position playback sites a minimum of one kilometer from a radio-collared individual. Subsequently, if a coyote was in the center of its territory (territories are $\sim 6.4 \text{ km}^2$), we broadcast playbacks near boundaries or outside territories; if a coyote was near a boundary, we

usually broadcast playbacks from within territories. Under these assumptions, we included coyotes' locations within coding for playback location. Finally, although radio-collared coyotes' locations were weighed when choosing nightly sites, we avoided using the same playback sites successively.

During playback sessions, we collected additional information on playback conditions. These included playback time, playback type, temperature, cloud cover, precipitation, barometric pressure, relative humidity, wind speed, wind direction, lunar cycle, and moon visibility.

Two to three sessions were conducted per night; each group vocalization (GYH and GH) session consisted of one to two playbacks per territory. We allowed a 15 minute waiting period following each playback, accounting for natural refractory time between vocalizations (Pimlott 1960; McCarley 1975; Harrington and Mech 1982; Lehner 1982; Harrington 1986).

In summary, a typical group vocalization playback session, lasting approximately 30 min, usually proceeded in the following manner: 1) a vehicle, used as mobile playback site, was parked approximately 1.6 km downwind of a radio-collared coyote or, if no radio-collared coyote was present, the vehicle was parked at a pre-designated site; 2) a coin was flipped to randomise the sequence of paired playbacks; 3) either a 40 s GYH or GH recording was broadcast from the vehicle after a 15 min waiting period; 4) all coyote

responses - including vocal response and locomotion - were monitored and recorded for 15 min after a playback; 4) a second playback was then broadcast 15-20 min after coyotes had resumed non-alert behaviour (e.g., no vocal response and restricted movement); and 6) data were recorded using procedures identical to the first playback. Again, lone howl playback sessions were conducted in a similar fashion, however playbacks were not paired.

Definition of Terms

Seasons were designated as breeding (15 Dec - 01 Mar), denning (includes whelping, 02 Mar - 15 May), pup-rearing (16 May - 15 Sep), and dispersal (16 Sep - 14 Dec).

Playback times were categorized as: period 1 (1600 - 2100), period 2 (2100 - 2400), period 3 (2400 - 0400), and period 4 (0400 - 0900).

For the purposes of this study, resident animals represent territorial residents and not solitary residents (Crabtree 1989). Playbacks locations were based on Crabtree's (1989) definition of resident coyotes' range sizes: within-territory playback sites were located within an area defined by the 0.001 probability contour for resident coyotes on the ALE Reserve. Likewise, those playback sites located outside the 0.001 probability contours of resident coyotes were grouped together, including playbacks broadcast along territorial boundaries, and those broadcast outside of a territory. Although we

predicated our definition of territory sizes upon spring ranges, winter and fall ranges also contained these central spring ranges; the size of this area averaged 75% of the total utilization distribution (Crabtree 1989).

We measured environmental parameters as follows: temperature in degrees celsius, cloud cover using 100% as total cloud cover, barometric pressure in cm taken from hourly meteorological reports, relative humidity in percentages taken from hourly meteorological reports and sling psychrometer readings, and wind speed using a styrofoam ball wind guage.

Environmental factors were categorized as follows: 1) wind - 0-8kph, 9-16kph, or >16kph; 2) barometric pressure - 25.4 cm increments; 3) humidity - 10% increments; 4) moon illumination - yes or no; and 5) precipitation - ranging from 1 through 4, none to heavy precipitation.

Data Analysis

Coyote vocalizations, described as a graded continuum both within and between vocal types, vary in intensity of communication through change in amplitude, frequency, or vocalization type (Lehner 1978a; 1978b). Consequently, these vocalizations are complex and greatly varied. We digitized and stored coyote vocalizations in ASCII format. ILS, a software system with capabilities for digital

signal and speech processing, enabled us to plot vocalizations in three-dimensional graphic display, as well as spectrally analyse vocalizations. These graphic displays depicted field and playback recordings, and produced frequency and amplitude profiles of GYH, GH, and lone howl vocalizations.

The data, primarily of categorical nature, were analysed with the SAS statistical program. Limited sample sizes frequently restricted the analysis to two-way interaction effects on response variables. As a result, we did not analyse three-way interactions (and greater) and were often forced to collapse categories down to fewer numbers. Because of the data's limitations, readers should be aware that pseudoreplication may be a problem when drawing inferences from resultant statistics (Hurlbert 1984).

Primarily, we focused on response to playback: vocal response and movement elicited per playback site. Vocal response was defined as a yes (1) or no (0) response to a playback; movement was defined similarly as a yes or no response. Hence, a playback may elicit 5 types of vocal response and two types of movement, however the playback was given a vocal response of 1 and a movement of 1.

Secondarily, we examined types of vocal response and movement. For summary statistics, all response types (6 vocalization and 5 movement categories) were surveyed. When statistically analysing response types, vocal responses were

categorized as either individual or group vocalizations; movement types were grouped into either advance or retreat from playback site. All responses, including vocalization and movement, and vocal and movement type were expressed as proportion responding; thus responses are reported as decimals <1.0.

A chi-square test of homogeneity and a likelihood ratio chi-square statistic (G^2 , a measure of association based on chi-square) were generated to analyse the effect of playback order on response (both vocal and movement); to compare response to GYH with that of GH playback; and to compare response to lone howl versus group vocalization (GYH and GH) playback. We analysed the effect of season, playback time, playback location, and territory on response using Weighted Least Squares (WLS) method. Often used for the analysis of multidimensional contingency tables, WLS technique combines matrices with a linear model approach (Forthofer and Lehnen 1981). Specifically, we analysed interactions (e.g., between season and playback type) using WLS and a specified contrast approach. Logit linear models were used when analysing the effect of environmental factors on response. Once a logit model was generated with an adequate likelihood ratio ($P > 0.25$), we next analysed such models using the WLS method.

Unless otherwise specified, we designated P-values as follows: $P < 0.001$ as highly significant; $P < 0.05$ as significant; and $P < 0.10$ as slightly significant.

Results

Between August 1987 and August 1988, approximately 650 group vocalization playbacks, including group howl (GH) and group yip-howl (GYH) recordings, were broadcast on the ALE Reserve. An additional 46 lone howl (LH) and 12 noise playbacks were broadcast between April 1988 and September 1988.

We generated digital sonagrams and frequency spectrums for 12 LHs, 8 GHs, 15 GYHs, and 9 GHs progressing into GYHs. In general, spectral analysis revealed that coyotes vocalize within a 1-3 kHz frequency range: LHs commonly peaked at 1-2.5 kHz (Fig. 2), GHs peaked at both 1 and 3 kHz (Fig. 3), and GYHs peaked also at 1 and 3 kHz with yips filling the range between 1 and 3 kHz (Fig. 4).

Comparison Within Paired Playback

This section addresses results of paired group vocalization (GH and GYH) playback, including vocal response, movement response, combined response, vocalization type, and movement type.

Group vocalization playbacks elicited a total of 321 vocalizations (OBS=1101) and 436 movements (OBS=790) over a one-year period. Of the vocalizations, 28.9% of the response were LHs, 24.5% were GHs, 24.5% were GYH-types

(including 66 GYHs and 13 GHs escalating to GYHs), 9.0% were bark-howls, and 4.9% were barks 4.9% (Table I). The average latency for vocal response was 0.97 min (SD=0.61).

In response to group vocalization playbacks, we most often observed movement toward a playback stimulus, including 197 advances (45.2% of elicited movement). Coyotes moved away from playbacks on 106 occasions (24.3% of elicited movement), and moved downwind on 26 occasions (6.0% of elicited movement). Additionally, we documented alpha animals moving together on 20 separate occasions (2 radio-collared alpha pairs). We consolidated all other movements: a total of 73 miscellaneous movements were elicited during group playback sessions (16.7% of elicited movement) (Table II).

The order in which group vocalizations were played significantly affected vocal response, but did not significantly affect movement. Group vocalization playbacks elicited significantly higher vocal response to first than to second playbacks ($N=661$; $X^2=14.12$, $df=1$, $P<0.001$). In contrast, group vocalization playbacks elicited similar movement to first and second playbacks ($N=460$; $X^2=0.04$, $df=1$, $P=0.85$). Because playback order differentially affected vocal response and movement, we subsequently analysed these response variables separately. Accordingly, vocal response was further analysed using only first playback data; movement was analysed using both first and second playback data.

Vocal Response

Group vocalizations were played to radio-collared coyotes with estimated home ranges, as well as to uncollared coyotes with unknown home ranges. Thus, we compared vocal response of territories with radio-collared animals to that of areas with no collared animals. Both radio-collared and non-collared territories responded to group vocalization playbacks with similar vocal response (first playbacks only; $N=333$; $X^2=0.92$, $df=1$, $P=0.34$). Hence, sites containing radio-collared and non-collared animals were pooled for this analysis.

Group vocalization playbacks elicited a vocal response 41.7% of the time ($N=335$). Vocal responses to playbacks did not differ significantly between seasons ($N=335$; $X^2=2.08$, $df=3$, $P=0.56$, WLS); between months ($N=335$; $X^2=11.0$, $df=11$, $P=0.44$, WLS); between time of playback ($N=327$; $X^2=5.41$, $df=3$, $P=0.14$, WLS); or between territories (radio-collared coyotes only, $N=149$; $X^2=6.75$, $df=7$, $P=0.5$, WLS). Moreover, frequency of vocal responses did not differ significantly between a GYH versus a GH ($N=333$; $X^2=0.08$, $df=1$, $P=0.77$); nor to foreign, non-neighbour, or neighbour vocalizations ($N=149$; $X^2=0.62$, $df=2$, $P=0.73$, WLS). However, coyotes did vocalize slightly more often to playbacks broadcast inside territories, than to playbacks broadcast along territorial boundaries or outside their territories (territories with radio-collared coyotes only, $N=166$; $X^2=2.63$, $df=1$, $P=0.11$,

WLS). Further, response relative to playback location was not affected by season nor playback type ($N=151$, $N=150$; $df=3$, $df=1$; $X^2=0.70$, $X^2=1.47$; $P=0.87$, $P=0.23$, respectively).

Environmental factors such as wind, presence or absence of moonlight, barometric pressure, humidity, or precipitation did not significantly affect coyotes' vocal response to playback (Table III). However, humidity did slightly affect vocal response: coyotes vocally responded more often during periods of humidity greater than 90%, but vocalized variably relative to other humidity categories ($N=320$; $X^2=12.88$, $df=8$, $P=0.12$, WLS). Highest humidities occurred most often during pre-breeding and breeding season; thus, high vocal responses may reflect effects of both humidity and time of year. Due to small sample size, we were unable to address this two-way interaction.

Although we detected no significant difference in vocal response in an overall seasonal comparison, coyotes showed a differential response to GYH and GH playbacks in the pup-rearing season. Specifically, during the pup-rearing season coyotes vocalized significantly more often to GYH than to GH playback, with no significant difference between playback type within other seasons ($N=333$; $X^2=5.39$, $df=1$, $P=0.02$, WLS, specified contrast) (Fig. 5).

Movement Response

Group vocalization playbacks elicited movement responses 56.2% of the time. Coyotes moved in response to playbacks with no significant difference between seasons ($N=439$; $X^2=5.52$, $df=3$, $P=0.14$, WLS), or between time of playback ($N=433$; $X^2=3.80$, $df=3$, $P=0.28$, WLS). However, coyotes' movement varied slightly between months ($N=439$; $X^2=17.61$, $df=11$, $P=0.09$, WLS), and between territories ($N=123$; $X^2=11.43$, $df=7$, $P=0.12$, WLS). Again, coyotes showed no significant difference in movement to GYH versus GH playbacks ($N=437$; $X^2=1.78$, $df=1$, $P=0.18$), nor in movement in response to foreign, non-neighbour, or neighbour playbacks ($N=389$; $X^2=3.52$, $df=2$, $P=0.17$). However, resident coyotes moved significantly more often in response to playbacks broadcast inside territories, than to playbacks broadcast along territorial boundaries, or outside their territories ($N=340$; $X^2=4.20$, $df=1$, $P=0.04$, WLS); response relative to playback location was not affected by season nor by playback type ($N=340$, $N=338$; $df=3$, $df=1$; $X^2=1.50$, $X^2=1.09$; $P=0.68$, $P=0.30$, respectively).

Most environmental factors (presence or absence of moonlight, barometric pressure, humidity, and precipitation) did not significantly affect coyotes' movement in response to playback. However, one variable, wind, did significantly affect movement ($N=438$; $X^2=6.91$, $df=2$, $P=0.03$, WLS) (Table III). Regarding the three categories, <8 km/hr, <18 km/hr, or >18 km/hr, coyotes moved most often to playbacks

broadcast in winds 8-18 km/hr, and moved least often to playbacks broadcast in winds greater than 16 km/hr.

Coyotes' movement revealed a similar pattern to their vocal response to group vocalizations: coyotes did not show an overall seasonal difference in movement, yet they did show a differential response to GYH and GH playbacks within seasons. In this case, coyotes moved more often to GYH than to GH playback during breeding season, with no significant difference between playback type within other seasons ($N=437$; $X^2=5.77$, $df=1$, $P=0.02$, WLS, specified contrast). Further, movement in response to group yip-howls was different from denning season ($N=437$; $X^2=8.69$, $df=1$, $P=0.003$, WLS, specified contrast), and from all other seasons ($N=437$; $X^2=3.96$, $df=1$, $P=0.05$, WLS, specified contrast) (Fig. 6).

Combined Vocal and Movement Response

We further combined vocal response with movement (playback elicited either a vocal response, a movement, or both) for further data analysis. Notably, coyotes responded to playbacks with either movement or vocalization at a high rate, 73% of the time. Moreover, overall responses were affected by season: coyotes responded slightly less often ($N=231$; $X^2=6.92$, $df=3$, $P=0.07$) during pup-rearing season than any other season (Table III).

Type of Vocal Response

Coyotes' type of vocal response to paired playbacks, categorized as either individual or group vocalizations, did not differ significantly with type or time of playback. However, type of vocalizations differed slightly in an overall seasonal comparison ($N=184$; $X^2=6.16$, $df=3$, $P=0.10$). In general, coyotes vocalized in groups more often during breeding season (61.7% group versus 38.3% lone vocalizations), and more often as lone individuals during denning season (61.2% lone versus 38.8% group vocalizations).

Type of Movement

Although coyotes' movement did not differ significantly between first and second playbacks, their type of movement, defined as either an approach or a retreat, did differ significantly ($N=176$; $X^2=4.53$, $G^2=4.55$, $df=1$, $P=0.03$). Principally, study animals more often approached after hearing the first playback (68.5% of movement), whereas they either approached or retreated from the stimulus after hearing the second playback.

Because order significantly affected coyotes' type of movement, we were unable to pool all playbacks for subsequent analysis. The resultant meager sample size revealed no seasonal trend in type of movement ($N=89$; $X^2=1.93$, $df=3$, $P=0.59$, WLS), nor showed an effect due to playback time ($N=87$; $X^2=3.06$, $df=3$, $P=0.38$, WLS), type

($N=88$; $X^2=0.53$, $df=1$, $P=0.47$, WLS), or location ($N=59$; $X^2=0.37$, $df=1$, $P=0.55$, WLS).

Lone Howl Playback

Lone howl playback elicited a total of 32 vocalizations and 88 movements. Both LH and GH vocalizations accounted for 28.1% of the elicited vocalizations; 9 LH and 9 GH vocalizations were elicited. GYH-type vocalizations accounted for 25.0% of all vocal responses, including 5 GYHs, and 3 GHs escalating into GYHs.

Regarding movements, LH playbacks elicited 34 advances (38.6% of elicited movement), 10 retreats (11.4% of elicited movement), and 13 downwind movements (14.8% of elicited movement). Additionally, we observed 18 miscellaneous movements in response to LH playbacks.

Coyotes did not appear to distinguish between LH recordings of pack members (including themselves), neighbours, or non-neighbours. For example, resident animals vocally responded to neighbour and non-neighbour LHs as often as they vocalized to their own LHs ($N=43$; $X^2=1.28$, $df=2$, $P=0.53$, WLS). Additionally, coyotes moved as often to neighbour and non-neighbour LHs as they moved to their own lone howls ($N=43$; $X^2=0.91$, $df=2$, $P=0.64$, WLS).

When comparing coyotes' response to LH versus group vocalization playbacks, we found that radio-collared coyotes did not vocalize significantly more to lone than to group vocalizations ($N=160$; $X^2=0.05$, $df=1$, $P=0.83$). However,

study animals did move significantly more often to LH than to group vocalization playbacks (N=215; $\chi^2=5.34$, $df=1$, $P=0.02$). Further, when elicited movement was compared for LH versus GH versus GYH playbacks, coyotes apparently moved less often to GHs than to LH or GYH playbacks (N=215; $\chi^2=6.70$, $df=1$, $P=0.01$).

We chose not to compare response types (e.g., vocal and movement types) elicited by lone and group vocalization playbacks. Sample sizes were too small for three-way comparisons (or greater).

Noise Playback

Noise playback, broadcast randomly during the denning and pup-rearing seasons, elicited no vocal or movement response. Noise playback elicited significantly fewer vocal responses than either LH or group vocalization playbacks (N=55, N=184; $\chi^2=14.8$, $\chi^2=14.95$ for both; $df=1$, $P<0.001$, respectively). For example, during a recording session (off the study area) in which we had elicited numerous vocal responses from 4 consecutive playbacks, we then broadcast a noise playback and elicited no response. We next broadcast another group vocalization 15 min following the noise playback, and again elicited vocal response. Hence, coyotes essentially did not respond to noise playback.

Habituation

Throughout the field period, we attempted to control for the quality of recordings, the effects of speaker placement, the effects of playback time, the possibility of habituation (Kroodsma 1989), and the effects of playback location. Because we conducted playback experiments over a one year period, habituation was a primary concern of this study.

Although habituation is difficult to detect, investigative measures were taken during data analysis to determine if coyotes had habituated to playback. Primarily, we reviewed response rates (both vocal and movement) over the year: if animals were habituating to our recordings, we would expect waning vocal response over time, and dwindling movement or more predictable movement patterns (e.g., movement away from playback) over time.

In surveying response rates, overall vocalization rates waned in December 1987, and April, May, and June 1988, revealing a pattern of dwindling response through the latter three months. However, vocal response again increased during late July and August 1988. Thus, we suspect the waning of response rates near the end of the study reflected seasonal effects. Additionally, elicited movements showed no dwindling pattern over time; neither movement rate nor movement type revealed any temporal trend. In short, we did not detect a progressive decrease in overall responsiveness

to playback, and therefore conclude that study animals did not habituate.

Discussion

Coyote communication is characterized as being graded, combined, and dynamic, hence is considered relatively complex (Lehner 1978a). The frequency, distribution, and intensity of coyote howling may communicate information about population density, social status of individuals (e.g., resident or transient), sex of individuals, and possibly age structure (Barnum et al. 1987). Although we were unable to investigate specific types of information communicated during howling bouts, we were able to examine overall responses to certain types of vocalizations, under varying conditions.

For example, resident coyotes on the ALE Reserve appeared to respond to vocal stimuli differentially, according to the time of year: coyotes seasonally distinguished between group vocalizations, moved to lone howls more than group vocalizations during pup-rearing season, and responded more often with communal howling during breeding season. Regardless of season or playback type, resident animals appeared to respond more often to playbacks broadcast within territories, than to those broadcast along or outside territorial boundaries.

Notably, resident coyotes did not respond differently to playbacks of neighbours, non-neighbours, or foreign coyotes. Although recognition of neighbours has not been investigated in canids, numerous studies have demonstrated that passerine birds discriminate between the songs of neighbours and non-neighbours (Emlen 1971; Brooks and Falls 1975; Kroodsmá 1976; Wunderle 1978; Weary et al. 1987). Territorial primates may also distinguish between neighbours and non-neighbours (Raemaekers and Raemaekers 1986). Because the ALE Reserve coyotes did not appear to differentiate between neighbours and non-neighbours, recognition of individual packs may be less important than the information conveying the location of an intruding pack (Lehner 1978b). Hence, study results support Lehner's (1978b) view regarding coyote vocalizations: the variation and gradation observed in LHs, GHs and GYHs may provide information through intensity of communication, while sacrificing individual recognition.

Seasonal Variation: Vocal Reply and Movement

Seasonal increases in howling, principally during the breeding season, have been reported in canids, including black-backed jackals (*Canis mesomelas*) (Skead 1973), wolves (Harrington and Mech 1979), and coyotes (Young and Jackson 1951). The seasonal variations observed in coyote vocalization rates may reflect vital aspects of their communication (Laundre 1981).

Several studies have documented significant variation in coyotes' spontaneous vocalization rates, primarily noting an increase in February (Laundre 1981; Walsh and Inglis 1989), and increases in March, August, and November (Laundre 1981). Additionally, Laundre (1981) reported a marked decrease in spontaneous vocalization rates during April and May.

Regarding elicited vocalizations, Harrington and Mech (1979) observed a distinct increase in wolf vocal response rates during February and March, followed by a gradual decline through April, and extremely low response rates in May through July. On the ALE Reserve, elicited vocal response rates followed both the seasonal pattern of elicited wolf vocalizations (Harrington and Mech 1979) (Fig. 7.), and that of spontaneous coyote vocalizations (Laundre 1981). Indeed, we observed high vocal response rates January through March, a waning in vocal response in April through mid-July, followed by an increase in vocal response rate in late July and August.

Differences in vocalizations and movement rates, noted in monthly comparisons, are less obvious in seasonal comparison: no significant differences in either vocal reply or movement rates were found in overall seasonal comparisons. For instance, playbacks elicited higher vocal response rates during January, February, March, and September ($X=0.50$, $SD=0.06$). Breeding season (15 Dec - 01 Mar) vocalization rate ($X=0.45$), however, did not reflect

the peak rates observed: the high vocalization rates of later breeding season (February through mid-March) were masked by the exceptionally low vocalization rate of early breeding season (December).

Likewise, we recognized a distinct reduction in elicited vocalizations during April, May, June, July, October, and December ($X=0.34$, $SD=0.06$). Again, the denning season (02 Mar - 15 May) vocalization rate ($X=0.46$) did not reflect the low rates of April and May: declining vocal response was masked by the exceptionally high vocalization rate observed in early denning (March). This, then, explains why we observed no significant difference between seasons in overall response rates. Moreover, it illustrates that response rates, especially vocal response, vary more within seasons than between seasons.

ALE Reserve coyotes responded with high vocalization rates January through March, corresponding with mid to late breeding season, and early denning season. Further, coyotes appeared to move most often to group vocalization playbacks during the breeding and denning seasons. Primarily, coyotes moved at peak rates during December (pre-breeding/breeding season) and April (denning season), and at relatively high rates in November (pre-breeding season), February (breeding season), and May (denning season).

During the breeding period, coyote group sizes may be greatest, primarily because of an increased sociality among adult pack members (Gese et al. 1988). This increase in

group size may, in turn, affect seasonal needs in communication (Bekoff and Wells 1980).

More specifically, during the winter months on the ALE Reserve, coyote social structure is extremely dynamic, undergoing a complex reassortment in social composition: territory sizes are still somewhat larger than the denning and pup-rearing periods, and territorial challenges may occur at this time (Crabtree 1989). During these months, the observed increase in elicited vocalization rate, the increase in elicited GH and GYH-type vocalizations, together with the high movement rates observed may reflect increased sociality within and between groups of resident coyotes.

Furthermore, coyotes may move greater distances and trespass more often during this season (Crabtree 1989); territorial activities may intensify with heightened boundary conflicts (Camenzind 1978). In summary, during breeding season intra-pack agonism may peak as packs reestablish social bonds and status; inter-pack agonism may peak as packs become less tolerant of neighbours (Harrington and Mech 1979). Thus, this increase in vocal and movement rate may reflect an increase in aggressive behaviour during the breeding season.

Typically, breeding coyotes responded to playbacks consistently, displaying little variation in either movement or vocal rate. In contrast, we observed great intra-seasonal variation in response during the denning season. For example, coyotes vocally responded at a high rate in

early denning (March), but vocally responded at decreasing rates in mid to late denning season (April through mid-June); movement response, however, remained high, peaking in May. During early denning, territories begin contracting (Crabtree 1989), group cohesiveness is maximized (Andelt 1985), and resident adults actively locate and excavate den sites in preparation for whelping; therefore, this peak in vocal response (March) may be associated with the well-defined social and spatial structuring of whelping period (our denning period) reported by Crabtree (1989).

Accordingly, the noticeable decrease in elicited vocal response during April and May could indicate the diversion of energy toward provisioning pups, and away from intensive territorial maintenance. For instance, after females whelp (April), territorial activity may lessen in boundary areas, yet may remain at high levels near active dens (Camenzind 1978); indeed, territory sizes on the ALE Reserve were significantly smaller during denning than all other periods (Crabtree 1989). On the ALE Reserve, coyotes begin whelping in mid-April and May; at this time, they begin provisioning pups and may not be vocally stimulated by inter-territorial announcements. Hence, waning vocal responses coupled with high movement rates may reflect stabilizing adult social structure, active pup-rearing, and lower-level territorial maintenance, post-whelping.

Most important, during the denning season, resident coyotes may cross boundaries and destroy resident

neighbours' litters (Camenzind 1976). Thus, denning coyotes' waning vocal responses and high movement rates may reflect their effort to protect newborn pups, while still moving to investigate potential intruders. Perhaps, denning coyotes, less willing to reveal their den and pup locations by vocalizing, actively protect offspring and maintain territories through movement.

During the pup-rearing season, resident coyotes vocalized and moved less to playbacks than during all other seasons. However, ALE Reserve coyotes distinguished between playback type more often than during other seasons. These results support the outcome of a study conducted in June through July 1975 near Jackson Hole, Wyoming, in which coyotes vocally responded more often to GYHs than to GHs (Lehner 1982). Hence, coyotes appear to distinguish between the two vocalizations during the pup-rearing season, although not during other seasons.

Based on the results of his research, Lehner (1982) hypothesized that the GYH serves primarily to announce occupancy of a territory, whereas the GH is principally an announcement of location. Because ALE Reserve coyotes appeared to distinguish (in vocal response) between these vocalizations during the pup-rearing season, we suggest that the functions of group vocalizations may vary according to resident coyotes' seasonal needs.

Early pup-rearing season (June and July) represents a time when resident coyotes defend smaller territories,

coyote social structure is less transitional, adults are spending much of their energy procuring food and caring for their pups, and resident coyotes are less likely to vocalize or move in response to stimuli (e.g., neighbours). Perhaps during pup-rearing season, high-intensity vocalizations such as the GYH, serve more as an intra-territorial form of communication, rather than as an inter-territorial signal of occupancy (i.e., playbacks, presumably simulating vocalizing neighbours, elicited few vocalizations during this period). In short, during pup-rearing season, adults may use GYH vocalizations primarily to strengthen social bonds (Ever 1968) and reaffirm social status among pack members (Lehner 1978a) (especially new pack members, such as pups), and secondarily to announce territorial occupancy.

Conversely, during breeding season coyotes may readily respond to numerous vocal stimuli by vocalizing and moving. Certain vocalizations may elicit more response, however detecting differential response at this time of year may be difficult. Indeed, though coyotes did not vocally respond more often to GYH playbacks, they did move more in response to GYHs during the breeding season. This may indicate that, during the breeding period, resident coyotes subtly distinguish between GHs and GYHs: they move more in response to GYHs, however vocal response to GYHs may be masked because coyotes are vocally responding to numerous types of vocal stimuli (e.g., LHs, GHs and GYHs). Further, during the breeding season, the group yip-howl may serve

primarily as territorial announcement, and secondarily to strengthen social bonds.

Finally, during dispersal period we again observed intra-seasonal variation: coyotes' movement to playbacks gradually increased as breeding season approached; however, vocal responses alternated monthly between highs and lows. Although coyote behavioural ecology is not well-documented for dispersal season, it appears to be a period of transition; dispersing pups become loners, joining a surplus of transient individuals who may prospectively contend for territories during breeding season (Crabtree 1989). Further, as social bonds between pups and alpha animals relax, adults may range greater distances and, in turn, display less predictable territorial behaviour (primarily, vocal response to neighbours). Thus, the observed variation in response may reflect the social transition of the pre-breeding period.

Environmental Effects

Several studies have reported that wind speed and barometric change affect coyote vocalization rates (Wolfe 1974; Wenger and Cringan 1978). Coyotes may vocally respond more often during periods of barometric change (Wolfe 1974); and may vocally respond less often in winds >16 km/hr (Wenger and Cringan 1978). Moon illumination does not appear to influence response rates (Wolfe 1974; Walsh and Inglis 1989).

We seldom broadcast playbacks in winds >20 km/hr (the estimated maximum speed in which we could still hear vocal responses). On the study site, winds of 16-14 km/hr were common and often localized, gusting at some locations and remaining calm at others. Although limited by sample size, ALE Reserve coyotes appeared to vocalize in high winds, as well as low winds. In general, resident coyotes may have experienced few days during which winds were calm.

We suggest that coyotes, capable of hearing vocalizations within a minimum 3.2 km radius, may vocalize in higher winds than commonly reported. For example, we conducted several field experiments to estimate maximum distances coyotes would respond to playbacks. Researchers were located at stations 3-6 km away from the playback site. On one occasion, those stationed at a 3 km distance heard elicited vocal responses, whereas the observer at the playback site heard nothing due to 24 km/hr winds. Thus, the coyotes may have been vocalizing during these windy periods, but our ears were incapable of hearing their vocal replies.

Coyotes moved more often during moderate winds (8-16 kph). We suspect coyotes were moving to reposition themselves for better auditory and olfactory reception (e.g., downwind of stimulus). Perhaps under calmer wind conditions, it was not energetically efficient for coyotes to relocate themselves: winds may not have been strong enough to enhance olfactory or auditory reception.

Likewise, during high winds, olfactory and auditory reception may be limited as scents and vocal signals are swiftly dispersed; thus, in both cases, movement may be an inefficient use of energy.

Lone Howl Vocalizations: Possible Functions

The coyote lone howl is a long-distance vocalization, used as a response to distant howling or spontaneously among separated group members; coyotes may howl to announce location, sometimes leading to the reunion of separated pack members. Further, lone howls may or may not reveal individual characteristics of the howler, and presumably serve different functions from that of the GH or GYH (Lehner 1978b).

Lone howls contain large variability in sound, including intra-howl and intra-individual variation; gradation in howls may demonstrate that coyotes have a large capacity for encoding information (Lehner 1978b). Lehner (1978b) questioned whether coyotes, like wolves, produce unique individual howls. Further, he proposed that the large intra-individual variation of howls might obscure inter-individual differences among coyotes.

We did not record enough individual lone howls to spectrographically demonstrate inter-individual differences. However, if coyotes do possess unique lone howls, we may expect pack members to respond to their own howls differently than neighbour or non-neighbour howls. Although

sample sizes were small, ALE Reserve coyotes responded to their own lone howls, both in movement and vocalization, similar to those of neighbours and non-neighbours. This may indicate that resident animals did not distinguish between their own howls and others.

But more probably, we may conclude that the large amount of information (possibly containing individuality, age, sex, social status, and emotional state) contained in a lone howl is not easily decoded, especially through recording the elicited responses of free-ranging coyotes. Moreover, lone howl recordings were sparse: we averaged only one or two recordings per territory; recordings, then, did not realistically represent the natural variability of individuals' lone howls. Thus, future research should focus on recording numerous lone howls for each individual coyote; should spectrally compare these howls within and between individuals; and should observe responses of both free-ranging and captive populations to lone howl playbacks.

Because sample sizes were small regarding lone howl experiments, study results must be cautiously reviewed. On the ALE Reserve, coyotes moved significantly more often, but did not vocalize significantly more often to lone howl than to group vocalization playbacks. Although not conclusive, coyotes' greater movement to lone howls suggests that lone howls may, indeed, communicate the location of the signaller, possibly within an unaggressive context. Movement may reflect repositioning of resident coyotes

relative to their location within their territories, to the signaller's location, and to the pups' locations within territories. Unfortunately, we were unable to analyse movement type in response to lone howl playback, information potentially crucial in yielding whether coyotes perceived playbacks as strangers or group members.

Interestingly, lone howls were the most common vocalization elicited, regardless of playback type (LH, GH, or GYH). This may suggest that coyotes use howls for more than simply announcement of location. Upon hearing a group vocalization playback, resident coyotes may invoke lone howl vocalizations as a low-intensity territorial announcement while simultaneously announcing location.

Principally, lone howls may serve this dual function when pack members are isolated and communal howling (even group howling) is improbable. Indeed, we observed several incidents in which one coyote responded to a group vocalization playback with a lone howl; immediately following a second playback, several coyotes would respond with a communal vocalization. Apparently, the resident coyote (whose movement was monitored) congregated with other coyotes to produce a higher intensity territorial announcement.

Thus, lone howls, along with group vocalizations, may serve multiple roles in coyote communication, especially on a seasonal basis. This is further supported by confounding study results: coyotes moved to LH and GYH playbacks with

similar response rates; responses to LH playbacks were least similar to GHs. Such results may again suggest that the lone howl may serve a role in low-level territorial maintenance, possibly only during pup-rearing season (LH playbacks were broadcast primarily during this period). Alternatively, these results more certainly reflect slight sample sizes.

Lone, group, and group yip-howls represent a graded continuum with each vocalization type serving different functions. Because these signals are graded, difference in function may be expressed through variation in frequency and amplitude, ultimately expressing intensity of communication (Lehner 1978b). Under these circumstances, we may expect the LH's function to be more similar to the GH's; likewise, the GH's function would be more similar to that of the GYH's. Study results, thus, did not strictly conform to this hypothesis. Due to the extreme complexity of coyote vocalizations, we are left with more questions than answers. Undoubtedly, further investigations of the lone howl will provide a broader basis for determining its function.

Group Vocalizations: Territorial Function

Territoriality, permitting ready access to crucial, economically-defendable resources (Brown 1964), is a prevalent phenomenon among coyotes on the ALE Reserve, a relatively unexploited, dense population of coyotes. Territorial coyotes may gain exclusive rights to resources,

in this case food and space, through either active displacement of intruders or passive avoidance of neighbours (Harrington and Mech 1983). Communal vocalizations, possibly a form of passive avoidance, may advertise territoriality by communicating pack locations and thereby minimising contact (Joslin 1967; Lehner 1978a, 1978b; Harrington and Mech 1979). Hence inter-territory vocalizing may serve a crucial role in spacing densely-packed groups within an area of limited resources.

On the ALE Reserve, resident pairs vocalized more and moved significantly more often to group vocalization playbacks broadcast within their territories than to those broadcast along boundaries or outside territories, regardless of season. Further, we recorded several instances in which resident coyotes, located peripherally within their ranges, repositioned themselves more toward their core ranges and sometimes vocalized after moving; we recorded no instances in which non-resident (radio-collared) coyotes vocalized in response to playbacks. Finally, coyotes tended to move rather than vocalize in response to intruders, presumably moving silently to investigate intruders without disclosing their locations.

Elicited behaviour of territorial canids is not well-studied. However, territorial avians may vocally or silently approach playbacks broadcast within their territories (Simpson 1984). Wolves may possess knowledge of spatial relationships within their territory (Peters 1978),

perceiving vocalizing intruders as a high-encounter risk (Harrington and Mech 1979). In general, ALE Reserve coyotes appeared to possess knowledge of spatial relationships. For instance, coyotes may have perceived a group vocalization located within their territory as an immediate threat, and therefore vocalized more often in passive territorial defence. More importantly, resident animals appeared to move more often to investigate these potential intruders.

Conversely, resident animals may have perceived more distant group vocalizations as less immediate threats. Indeed, a stranger vocalizing outside the residents' territory may represent a low-encounter risk (Harrington and Mech 1979). Thus, they may or may not vocally respond, but may use less proximate forms of passive territorial defence such as scent-marking. Again, immediate movement in response to this distant stimulus may not be imperative: trespassing outside core areas may be common (Crabtree 1989), and territorial defence of these outlying areas less urgent.

Wolf territorial behaviour has been intensively studied. For example, during a field experiment conducted by Harrington and Mech (1979), wolves reportedly approached the stimulus site only seven times in 1783 trials. Unlike the elicited movement pattern of wolves, coyotes commonly approached playbacks. However, they did not appear to approach or retreat relative to playback location, but more often took advantage of local wind conditions (e.g.,

circling downwind). Remarkably, we seldom observed a transient coyote approach the playback site; only on one occasion did a non-resident approach, however, she was accompanied by the associate resident of the territory. The approach movement pattern, therefore, may represent an important component of territorial maintenance for densely populated coyotes.

Wolves display territorial behaviour, primarily howling and secondarily scent-marking, which is location-independent (Harrington and Mech 1983). For example, wolves reply to human-simulated howls whether or not the intruder or the pack is located closer to the center of their territory. Because wolf howling-response is a territory-independent spacing mechanism (Harrington and Mech 1983), wolves must secure exclusive use of resources through strong (in this case, year-round) site-attachment, coupled with howling (Waser 1975, 1977; Harrington and Mech 1983).

In contrast, coyotes may display territory-dependent vocalizations. Indeed, coyotes appeared to respond to playbacks differentially, depending upon playback location. Within rigid ecological conditions, group vocalizations may serve as a territory-dependent spacing mechanism, primarily among densely populated coyotes with limited habitat and prey-base.

The importance of how a territorial animal perceives spatial relationships is well illustrated in a dense coyote population. For example, coyote territories on the ALE

Reserve are small, averaging 5.5 to 6.5 km². A coyote can readily cross the widest breadth of its territory within 30 min (J. Blatt, pers. commun.), and can hear neighbouring vocalizations within a 3.2 km radius. Within such limited space, it may be energetically efficient for coyotes to discern between imminent intrusion and distant, less-threatening encroachment (e.g., neighbours). Hence, territory-dependent avoidance mechanisms, such as vocalizations and possibly scent-marking, as well as high seasonal site-fidelity, enable coyotes on the ALE Reserve to maintain exclusive territories.

Conclusion

In summary, ALE Reserve resident coyotes' responses to playbacks varied, principally according to season. Coyotes responded (with either movement or vocal reply) most often to playbacks during the breeding season, a period characterized by high sociality and inter-group agonism. Coyotes responded least often during the pup-rearing season, however during this season they appeared to vocalize more often to GYH than to GH playbacks; further, they moved significantly more to LH than to group vocalization (i.e., GH or GYH) playbacks. We observed pronounced intra-seasonal variation in coyote response during the denning and dispersal seasons.

Resident coyotes appeared to distinguish between high-risk (i.e., playbacks broadcast within core territories) and

low-risk encounters (i.e., playbacks broadcast outside core territories), vocalizing more and moving significantly more often to territorial intruders. This implies that coyotes may command knowledge of spatial relationships, relying on group vocalizations for territorial spacing and mutual avoidance between territorial groups.

Coyotes possess a highly evolved auditory communication system. This research only cursorily investigated the possible functions of three vocalizations (LHs, GHs, and GYHs) in one coyote population. Thus, future research should emphasize the functions of such vocalizations under varying social conditions, including lightly exploited and heavily exploited populations. In contrasting the social structure within which coyotes vocalize, we may gain a better understanding of the territorial function of vocalizations as well as the behavioural ecology of coyotes.

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Table I. Summary of elicited vocalization types.

		Elicited Vocal Responses									
Playback	B	BH	LN	CH	GYH	GH/ GYH	Misc	Total (0/1)		Total	
								Resp	No Resp	PBs	PBs
Group Voc (GH/GYH)	16	29	93	79	66	13	25	321	230	431	661
Lone Howl	1	1	9	9	5	3	4	32	15	28	48

Table II. Summary of elicited movement types.

		Elicited Movement											
		To/		Down		Move		Total		(0/1)		Total	
Playback		Away		wind		in		N		Resp		Total	
PB		PB		PB		Pairs		Misc		Resp		PBs	
PB		PB		PB		PBs		Resp		No Resp		PBs	
Group Voc (GH/GYH)	197	106	14	26	20	20	73	436	250	210	460		
Lone Howl	34	10	10	13	3	18	88	27	16	48			

Table III. Elicited vocalization and movement compared with independent variables (group vocalization playback only).

Independent Variable	N		Vocal Resp		Move Resp		Combine	
	(0/1)	(0/1)	P-value	(0/1)	P-value	(0/1)	P-value	Voc/Mov (0/1) p-Value
Season	335	439	0.556	439	0.138	231	0.075+	
Month	335	439	0.443	439	0.091+	231	0.581	
Playback Time	327	433	0.144	433	0.284	227	0.300	
Playback Type (GH vs. GYH)								
Overall	333	437	0.774	437	0.182	230	0.545	
Seasonal	333	437	0.020*	437	0.016*	.	.	
Playback Location	161	309	0.110	309	0.040*	.	.	
Territory	149	123	0.456	123	0.121	.	.	
Neighbour/Non-neighbour	149	389	0.730	389	0.170	.	.	
Environmental Factors								
Wind	320	436	0.632	436	0.032*	.	.	
Moon	320	438	0.138	438	0.306	.	.	
Humidity	319	438	0.116	438	0.286	.	.	
Barometric Press.	319	436	0.536	436	0.849	.	.	
Precipitation	320	438	0.849	438	0.782	.	.	

+Slightly Significant
*Significant

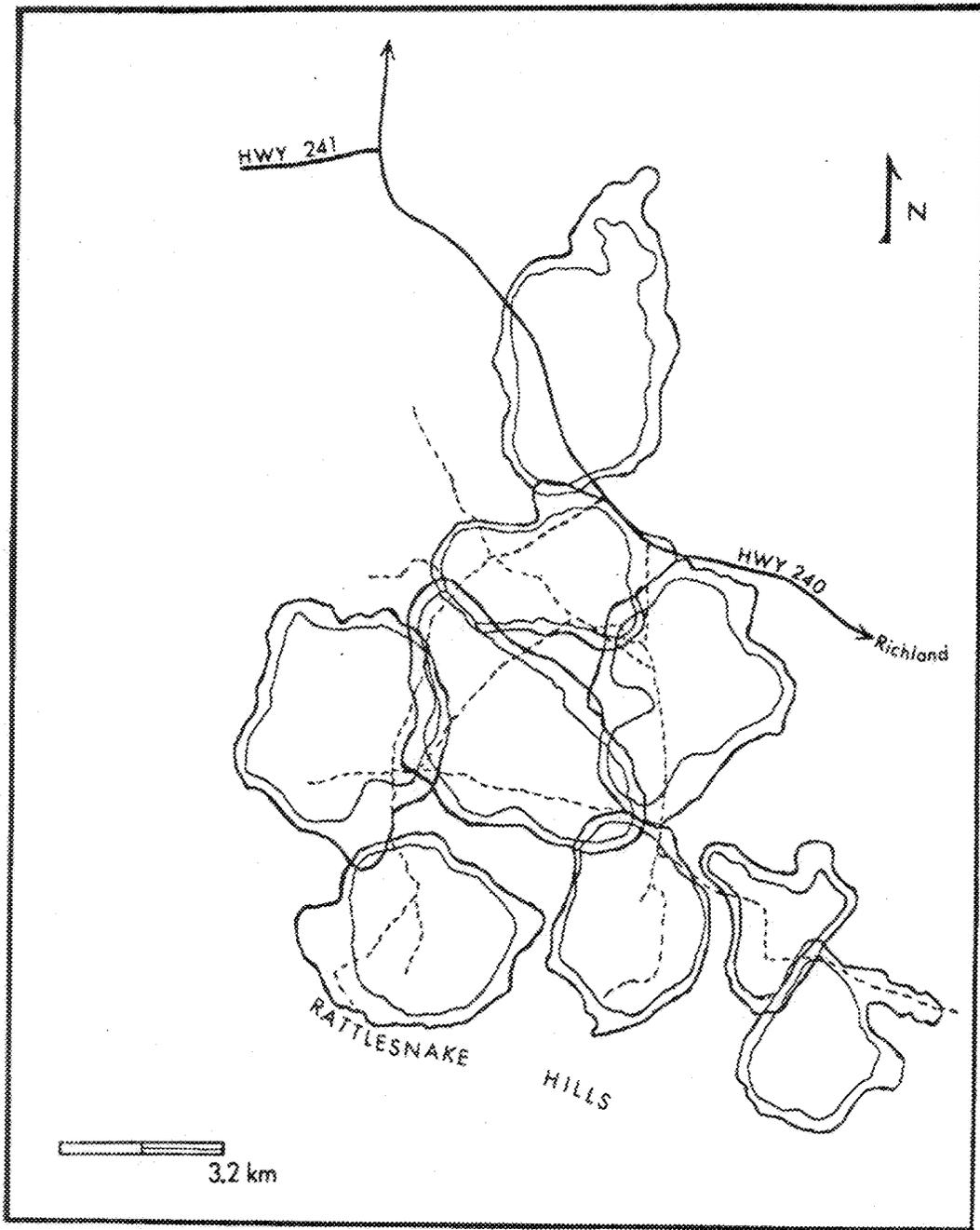


Figure 1

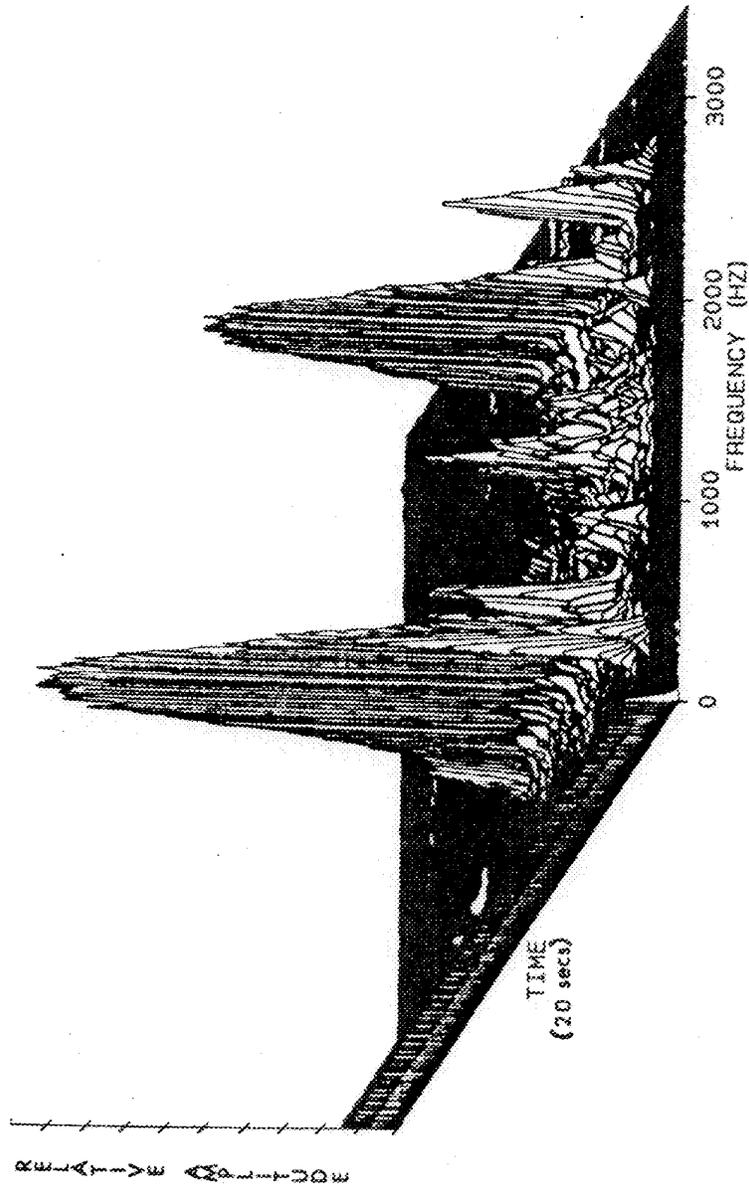


Figure 2

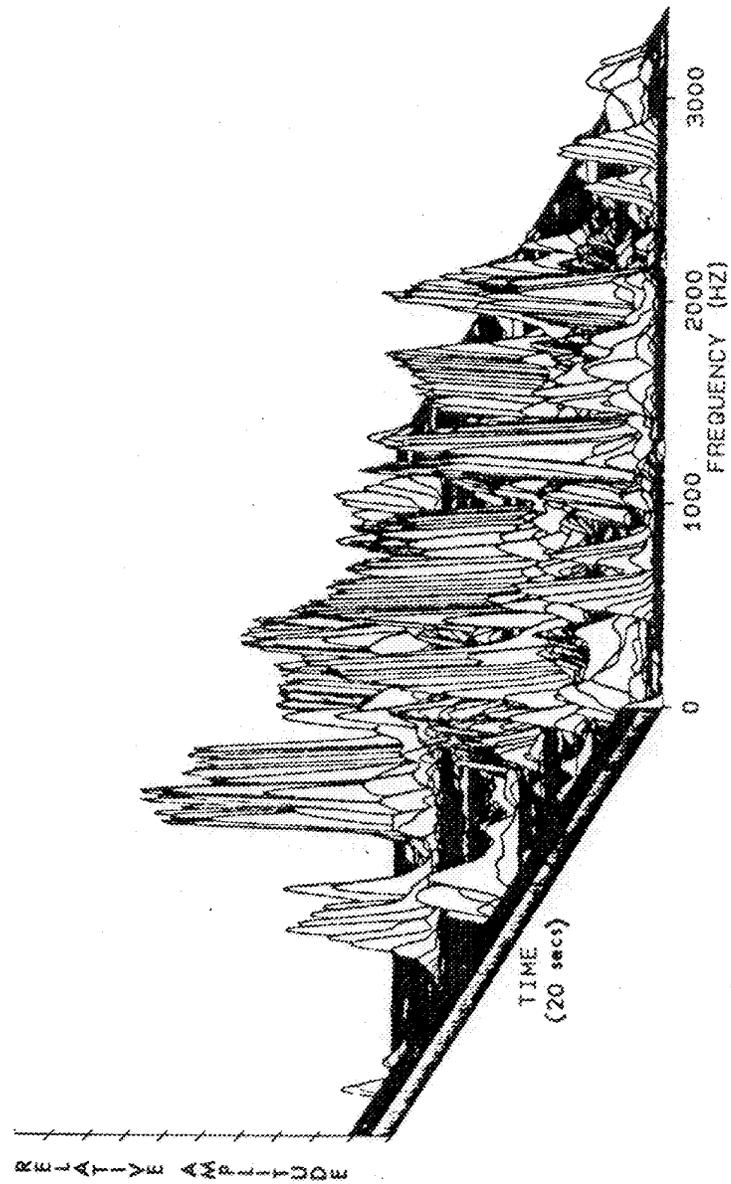


Figure 3

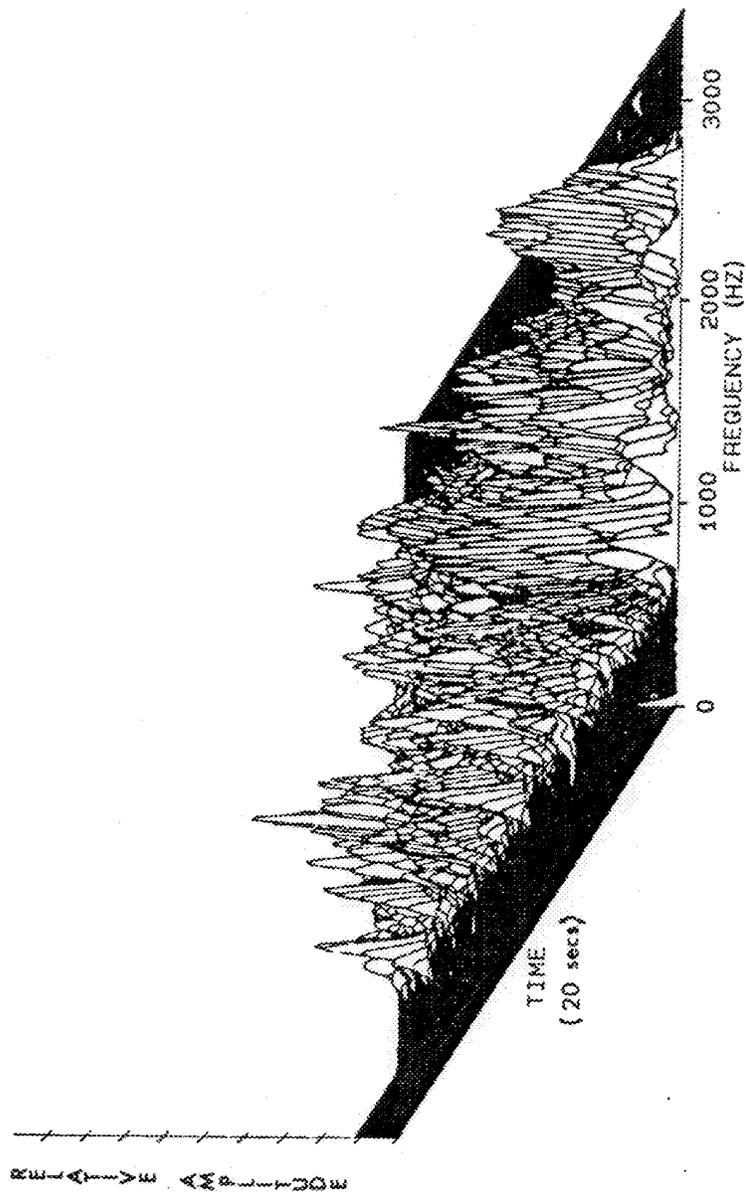


Figure 4

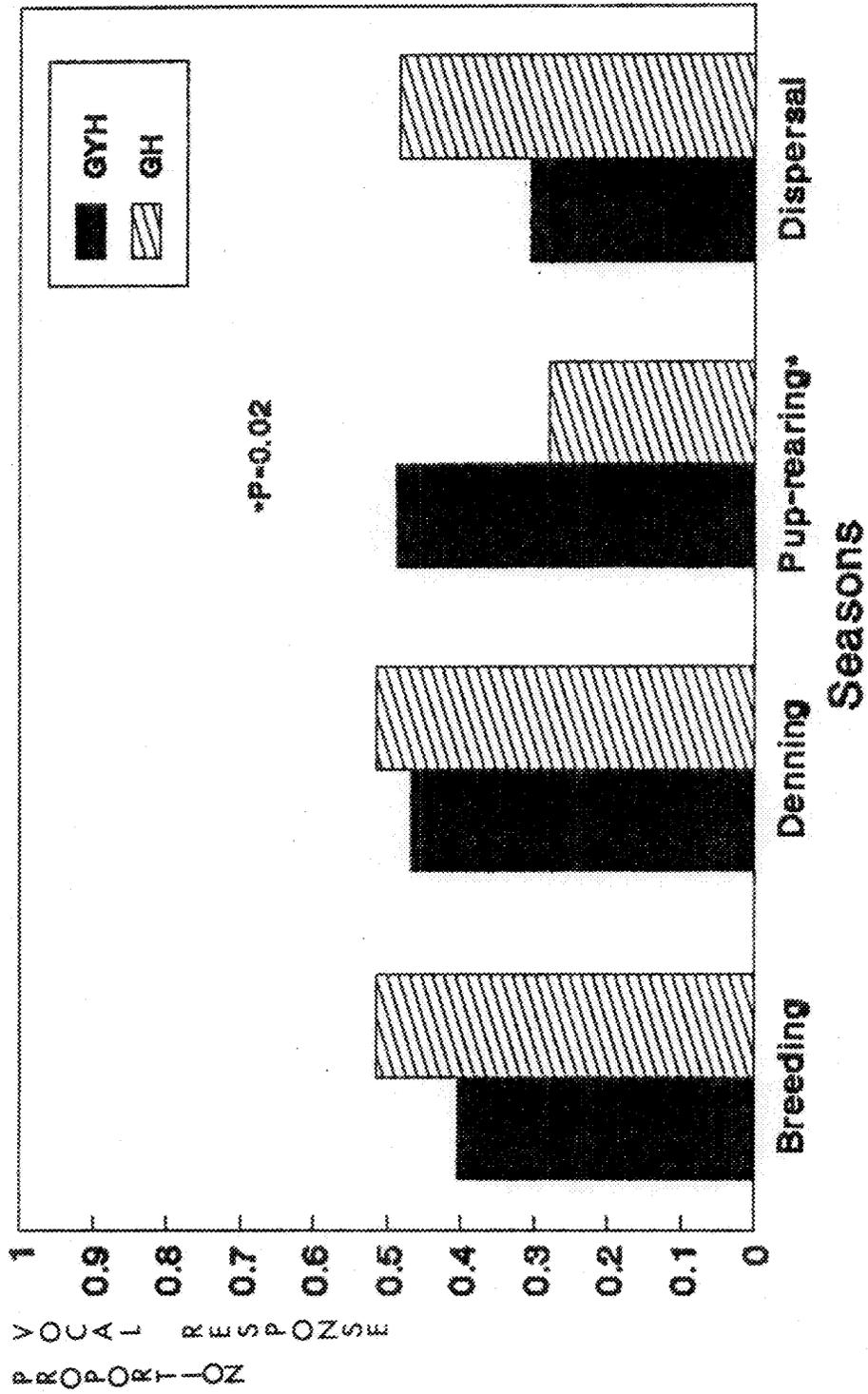


Figure 5

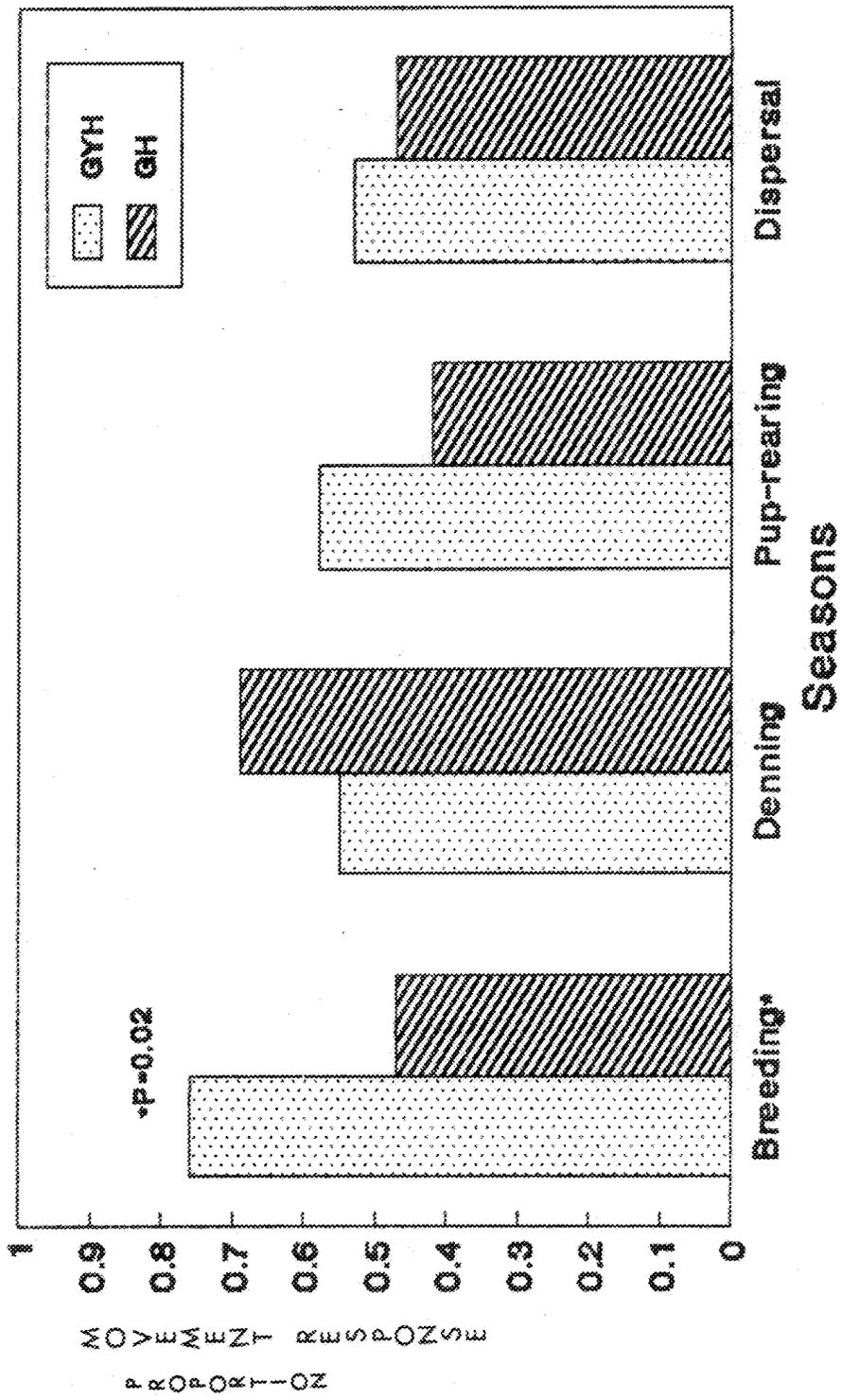


Figure 6

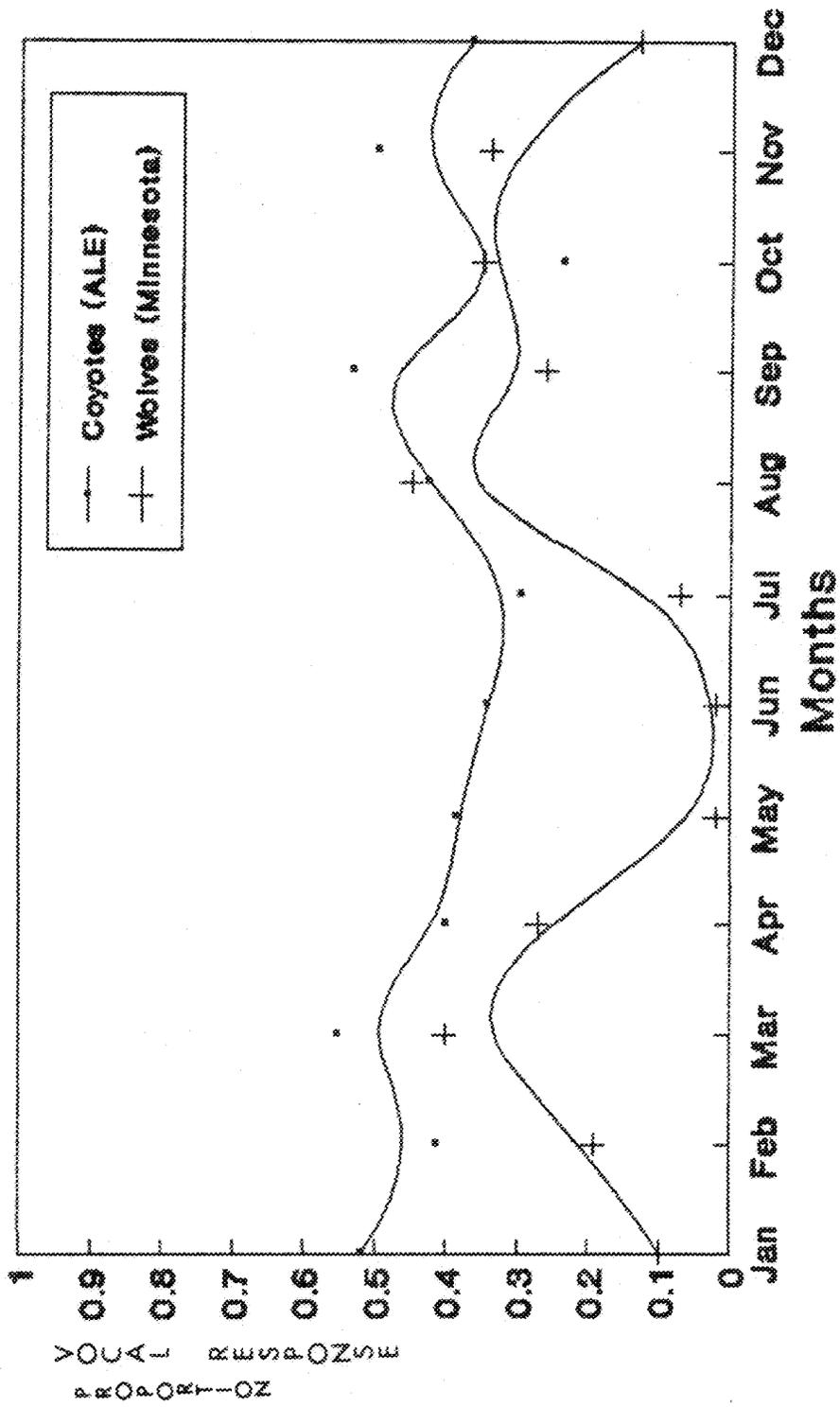


Figure 7

APPENDIX A
STUDY OBJECTIVES & NULL HYPOTHESES

- Objective 1: To compare territorial coyotes' responses (vocal reply and movement) to GYH and GH playbacks.
- Objective 2: To compare between territorial coyotes' responses to LH versus GYH and GH playbacks (playbacks of group vocalizations).
- Objective 3: To compare territorial coyotes' responses to GH and GYH playbacks broadcast within territories versus those broadcast outside territories.
- Objective 4: To compare territorial coyotes' responses to GH and GYH playbacks between seasons, including breeding, denning, pup-rearing, and dispersal periods.
- Objective 5: To determine if correlations exist between coyotes' responses to GH/GYH playbacks and key environmental factors (i.e., wind speed, cloud cover, precipitation, barometric pressure, relative humidity, and lunar cycle).
- Objective 6: To determine whether coyotes' responses to playbacks can be used to better characterize the role of group vocalizations in territorial maintenance.

APPENDIX A (continued)
NULL HYPOTHESES

1. H₀ Territorial groups respond (vocal reply or movement) identically to a GH and GYH playback (Objective 1).
2. H₀ Territorial groups respond identically to a LH as to a GH and a GYH playback (Objective 2).
3. H₀ Territorial groups respond identically to GYHs and GHs played within their territories as to GYHs and GHs played outside their territories (Objective 3).
4. H₀ Playbacks of GYHs and GHs elicit identical responses during breeding, denning, pup-rearing, and dispersal periods (Objective 4).
5. H₀ Territorial groups respond equally to playback stimuli, regardless of the influence of key environmental factors, such as wind speed, cloud cover precipitation, barometric pressure, relative humidity, and lunar cycle (Objective 5).
6. H₀ Territorial groups' responses to PBs do not, in any way, characterize the role of group vocalizations in territorial maintenance (Objective 6).

APPENDIX B
LOCATION OF ARID LANDS ECOLOGY RESERVE (ALE)

