INFORMATION IN A LONG-DISTANCE VOCAL SIGNAL: CHORUS HOWLING IN THE COYOTE (*CANIS LATRANS*)

DISSERTATION

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By

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ABSTRACT

Fighting can be extremely costly in terms of energy use and potential for injury or death. Therefore, the ability to accurately assess a threat is advantageous, allowing an animal to retreat from conflict if its chances of winning are low. Game-theoretical models of agonistic behavior suggest that animals should base decisions about conflict escalation on an assessment of their opponent's fighting ability or resource-holding potential (RHP). Individuals can assess an opponent's fighting ability relative to their own using a number of physical and behavioral cues. Some aggressive displays, including some vocalizations, are believed to function as such cues, or advertisement displays, of an animal's RHP.

Studies of advertisement displays have typically focused on contests between individuals. However, just as correct assessment of a rival is advantageous in conflict-escalation decisions between individuals, it might be expected that correct assessment of group size would be an important criterion in determining potential costs in contests between groups. Social animals would benefit from accurate perception of group size when assessing the fighting ability or RHP of a competing group in the same way that individual competitors benefit from assessment of their single competitor's size and strength.

A number of studies have been published in recent years investigating group-level assessment in agonistic contests. These studies have focused on territorial vocal signals of various group-living species to determine whether competing groups glean information about group size from these acoustic signals and adjust their behavior in a manner consistent with the predictions of game-theoretical models of agonistic behavior.

The goal of this thesis research was to determine whether group-size information is available in the group yip-howl of the coyote. The approach to this investigation was two-fold: a) conduct a field experiment with radio-collared coyotes and measure their movement and vocal responses to playbacks of group yip-howl recordings from different-sized groups, and b) analyze the acoustic features of the coyote group yip-howl. The aim of the field playback experiment was to measure the responses of coyotes to the agonistic vocalizations of a potential competing group. Acoustic features of the coyote group yip-howl were analyzed to better understand the potential cues contained in the signal that might allow for the perception of group size.

Dedicated to my grandfather, Thomas Edward Alderdice (1912 – 1984)

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FIELDS OF STUDY

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CHAPTER 1

INTRODUCTION

Assessment of Rivals in Agonistic Contests

Fighting can be extremely costly in terms of energy use and potential for injury or death. Therefore, it is expected that animals will avoid entering into direct conflict unless the threat to their survival or reproductive success is so great as to inflict a greater cost than the conflict. Potential loss of a mate or a territory could represent such threats. With costs this high the ability to accurately assess a threat is advantageous, allowing an animal to retreat from conflict if it is unlikely to emerge the winner.

Game-theoretical models of agonistic behavior suggest that animals should base decisions about conflict escalation on an assessment of their opponent's fighting ability or resource-holding potential (RHP). A multitude of asymmetries can exist between individuals competing for possession of resources, including size and strength of each individual, current ownership of the resource, and the importance of the resource to each competitor. These asymmetries can aid in predicting the outcome of a conflict. Therefore, in competitions where fighting is costly, it is selectively advantageous for an animal to assess its chances of winning and withdraw without escalation if those chances are low (Enquist & Leimar, 1983; Hammerstein, 1981; Maynard Smith, 1982; Maynard Smith & Parker, 1976; Parker, 1974).

Some aggressive displays, including some vocalizations, are believed to function as advertisements of an animal's fighting ability or resource-holding power, allowing a competitor to assess its chance of winning in a direct conflict (Clutton-Brock & Albon, 1979; Parker, 1974). A multitude of behaviors and physical characteristics have evolved that allow animals to assess the condition and strength of an opponent relative to themselves. Some of these include: potential "weapons," such as antlers and canines, with greater size indicating better condition and potential to inflict injury (Darwin, 1850; Geist, 1971; Packer, 1977); broadside threat postures that display the largest physical profile and provide the best indication of size (Hinde, 1982); the pitch of a vocalization, with lower pitch indicating larger body size (Morton, 1977); and the frequency and duration of a physical or vocal display, with longer or more frequent displays indicating better condition (Clutton-Brock & Albon, 1979).

Studies of advertisement displays have typically focused on contests between individuals. However, just as correct assessment of a rival is advantageous in conflict-escalation decisions between individuals, it might be expected that correct assessment of group size would be an important criterion in determining potential costs in contests between groups. Social animals would benefit from accurate perception of group size when assessing the fighting ability or RHP of a competing group in the same way that individual competitors benefit from assessment of their single competitor's size and strength (McComb et al., 1994). Two important assumptions underlie this prediction: 1) signals communicating group size information are honest; and 2) animals can comprehend numerical differences in quantity.

Honest Communication and Numerical Competence

On average, animal communication signals are honest, meaning the information they convey accurately depicts the situation about which they are communicating. For example, the assessment criteria in agonistic contests described above (e.g., antler size, pitch of a vocalization, duration of a display) are closely linked with the individual's RHP or fighting ability (Clutton-Brock & Albon, 1979). Therefore, these physical cues and behavioral displays are honest indicators of the individual's ability to defend itself and its resource.

Dawkins and Krebs (1978) argued that game-theoretical models suggested that senders should try to mask their true intentions and manipulate receivers into acting in a manner that would benefit the sender. However, subsequent models have convincingly demonstrated that honest signaling should be the rule. Zahavi and Zahavi (1997) have put forth a compelling argument that receivers should not respond to dishonest signals: if receivers do not respond to a signal, then there is no benefit to senders to produce one. Zahavi's (1977) "handicap principle" further argued that heavy costs associated with signals impose honesty. That is, an individual could not afford to produce a signal or would not be physically capable of producing a signal if the information it contained were not accurate. For example, a peacock's tail is considered a handicap since it imposes costs by making the bird more vulnerable to predators and by being costly to develop physiologically. Therefore, the peacock's tail is an honest indication of the animal's condition (Zahavi, 1975).

Numerical competence in animals has been argued to exist in various forms, from a binary, there/not there discriminative ability to actual counting, using a "tagging" system like that used by humans (Davis, 1993). The majority of studies investigating animal numerical competence have been conducted in the laboratory, with the most support for true counting coming from experiments with non-human primates. However, the success (as limited as it has been) of these counting experiments has resulted from extensive training of the animals under complex, artificial conditions (Shettleworth, 1998). Despite disagreement on the specific numerical abilities of animals, there is little argument that animals have some ability to discriminate numerosity (Shettleworth, 1998). In natural settings, animals may only need to discriminate between relative quantities; and this ability may be especially important in species that live in social groups (Davis, 1993; McComb et al., 1994).

Studies of Group-Size Assessment in Agonistic Contests

A number of studies have been published in recent years investigating group-level assessment in agonistic contests. These studies have focused on territorial vocal signals of various group-living species to determine whether competing groups glean information about group size from these acoustic signals and adjust their behavior in a manner consistent with the predictions of game-theoretical models of agonistic behavior. Each of these studies employed a field playback paradigm, in which group territorial vocalizations of different-sized groups were broadcast and movement and vocal responses of the target (receiving) groups were measured.

McComb et al. (1994) studied the responses of female lions (*Panthera leo*) to playbacks of single female lions roaring and groups of three female lions roaring in chorus. They found that female lions adjusted their behavior based on the ratio of the intruder’s group size to their own, approaching only when odds were strongly in their favor. Parallel work conducted with male lions, however, indicated that males were less cautious and approached even when outnumbered by one to three individuals. McComb et al. attributed the difference in male and female responses to the sexes’ differential valuation of the territory with respect to their reproductive success. Accordingly, an increase in female approach was observed when cubs were present, reflecting the increased value of the resource in that circumstance.

Results similar to McComb et al.’s were found in male black howler monkeys (*Alouatta pigra*) (Kitchen, 2004), male chimpanzees (*Pan troglodytes*) (Wilson et al., 2001), and subdesert mesites (*Monias benschi*) (Seddon & Tobias, 2003). In each species, it appeared that numerical assessment of the intruding group’s size relative to the defender’s was an important factor in determining whether group members would approach and/or vocalize in response to the apparent invasion. Typically groups would not approach or vocalize in response to playbacks of groups larger than their own and would approach cautiously if odds were only slightly in their favor. Vocal responses were less common than approaches in most species, and in chimpanzees it appeared that vocalizing in response to the playback was more dependent on the number of defenders present than was approach movement (Wilson et al., 2001).

The studies described above focused primarily on the movement of the target animals in response to the playback stimuli. However, a study by Radford (2003) examined the vocal responses of green woodhoopoes (*Phoeniculus purpureus*) to playback of conspecific groups' territorial vocal rallying calls and compared these responses to spontaneous bouts of vocal rallying. Radford found that the duration of spontaneous vocal rallies was positively correlated with the size of the rallying group. However, bouts provoked by playback of a larger group were longer in duration than spontaneous rallies. Therefore, only spontaneous vocal rallies could be considered honest cues to group size.

Group Size Information in the Chorus Howling of Wolves and Coyotes

Coyotes (*Canis latrans*) are social, group-living carnivores, like wolves (*Canis lupus*). However, compared to wolves, coyote social groups are quite small, consisting of a breeding alpha pair and offspring from the current year (typically a litter of five or six), and often some of the previous year's offspring that have remained with their natal group as helpers. Breeding coyote pairs are territorial and defend a relatively small territory within a larger home range that can measure tens of square kilometers (see Chapter 2). Although the larger ranges of different coyote groups commonly overlap, core territory boundaries do not.

As with the species described in the studies above, coyotes also have a long-distance group vocalization: the group yip-howl. Howling is the primary long-distance signal among the species of the family Canidae, and pack members often howl in a chorus that is believed to announce territory ownership to neighboring groups and transients (Harrington & Mech, 1979; Lehner, 1978a, 1978b; Theberge & Falls, 1967). This inter-group signal, which often elicits responses from neighboring conspecific groups, is also believed to act as a spacing mechanism between groups (Harrington & Mech, 1979; Lehner 1978a, 1978b). However, whether chorus howls contain information about group size has been debated in the literature.

Harrington (1989) proposed that group howling in the gray wolf might be a mammalian example of the Beau Geste effect. The Beau Geste hypothesis was put forth by Krebs (1977) and named after a fictional French Foreign Legionnaire who successfully defended a fort single-handedly by imitating the voices of many men and leading his enemy to believe an entire army was present (Bradbury & Vehrencamp, 1998). Harrington suggested that the chorus howl of the wolf similarly deceives receivers, leading them to estimate that an area is occupied by a larger number of individuals than it actually is, or at least making exact number undetectable. Harrington suggested that the frequency modulation often introduced into group howls produces echoes as the sound travels through the environment, ultimately distorting the signal on the receiver's end and resulting in the perception of a greater number of callers than are actually present. He claimed that even canid research specialists cannot determine the number of individuals present in a group chorus from listening to the acoustic signal alone.

Harrington’s (1989) methods for investigating the question of group size information in howling choruses involved approaching radio-collared wolves within 200-800 m, howling to them using a “simulated howl,” recording the wolves’ vocal response on audiotape, and analyzing the spectrograms of these recordings. Unfortunately, it was impossible to distinguish individual animals in the spectrograms; once an individual howled, it could not be discerned whether it was the same or a different animal howling later in the chorus. Therefore, although Harrington based his Beau Geste hypothesis on this spectrographic analysis, his methods actually did not allow him to resolve whether potential patterns allowing for discrimination of group size exist within a howling chorus.

Lehner (1978b) proposed a quite different theory in his studies of coyote group howling. He suggested that coyotes, and possibly other canids that use similar chorus howls, are capable of assessing group size from a howling chorus based on differences in individual voices. He further suspected that this is an epideictic signal, allowing animals to assess the density of the local population, and thereby affecting their reproductive strategy directly or indirectly. Indirectly, group howling choruses, serving as territorial signals that allow groups to space themselves appropriately in the environment, might affect reproductive strategy in the sense that they reflect territory availability. However, Lehner (1978b) proposed that howling choruses might directly affect reproduction in a way similar to the Lee-Boot effect in rodents, where pheromones inhibit estrus cycles in captive females when the caged group is large (Turner, 1966). Of course, prey density likely directly regulates population density in conjunction with either of these processes.

It is also necessary to ask if the Beau Geste effect can exist in animal communication systems. The Beau Geste hypothesis was initially used to explain large repertoire size in territorial birds, claiming that these birds acquired large repertoires to mislead potential intruders into believing that more territory holders were present than there actually were (Bradbury and Vehrencamp, 1998). However, Bradbury and Vehrencamp (1998) reported that such song patterns in birds are not successful in deceiving potential intruders. Indeed, if a signal such as group howling consistently provided misleading information about group size, it would be expected that the signal would not be used to assess competitive ability, since it is unreliable in this function.

Lehner (1978b) suggested that coyotes may vocalize less when population numbers are low, which may serve as a cue indicating low population density. However, if this is true, it does not appear to translate to the coyote's signaling strategy when *group* size is small (i.e., with coyotes howling less when group number is low). Gese and Ruff (1998) found that howling rates were independent of pack size.

The structure of the coyote group yip-howl (the name applied to coyote chorus howling by Lehner (1978a, 1978b)), as it is described in the literature, suggests that information about group size might be available in the signal. Lehner (1978b) explained that "a group yip-howl bout is generally initiated by one individual… which is then joined by others. The initiator generally gives a long, relatively un-modulated howl. As more individuals join in, the howls become more amplitude and frequency modulated and yipping occurs, gradually becoming more frequent" (p. 718). This structural pattern can potentially reveal information about the number of howling participants. Two of the components in particular, timing of entry into the chorus and fundamental frequency (f_o) of an individual howl, could allow receivers to “hear out” the number of individuals howling. Research into the ability of humans to hear out separate sound sources has shown these features of sound to play an important role (Moore, 1997).

The sequential entry of individual voices into the chorus could allow listeners to discriminate the number of individuals vocalizing. Asynchrony in sound onset is a cue used by humans to hear out the sources of complex sound (Moore, 1997). Interestingly, Joslin (1967) used this feature of wolf chorus howls to estimate pack size by ear, and found it to be a method superior to any other he had employed.[1] In addition, Lehner (1978b) suggested that the initial howls in the chorus are also relatively constant in frequency; therefore, these sounds should propagate reliably through the environment. This signal design feature increases the long-distance reliability of the chorus as an indicator of group size.

It has been reported that individual wolves avoid howling at the same frequency as other individuals in a chorus (Boscagli, 1984; Crisler, 1958; Harrington, 1989; Lehner, 1978b). Fundamental frequency is a key feature used by humans to hear out individual sound sources. It has been found that people can distinguish between complex tones (e.g., those created by identical musical instruments) when each is playing a sound of a different f_o (Moore, 1997). In addition, it seems that this can best be achieved if the sounds differ in frequency by 6% (Scheffers, 1983). Tooze et al. (1990) used

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[1] However, like Harrington, he could only count the wolves as they initially entered the chorus. Thus, once an animal ended its first howl it could not be determined whether the same or a different individual entered the chorus later.

discriminant function analysis (DFA) to successfully identify the howls of individual wolves. The correct categorization of howls in their analysis was to a great extent dependent on the f_o.

Overview of Thesis Chapters

The goal of this thesis research was to determine whether group-size information is available in the group yip-howl of the coyote. The approach to this investigation was two-fold: a) conduct a field experiment with radio-collared coyotes and measure their movement and vocal responses to playbacks of group yip-howl recordings from different-sized groups, and b) analyze the acoustic features of the coyote group yip-howl.

The aim of the field playback experiment (described in Chapter 4) was similar to the objectives of the group-assessment studies with lions, howler monkeys, and chimpanzees described above: to measure the responses of group-living animals to vocalizations of potential competing groups. Target groups of radio-collared coyotes were tested with two playback conditions: a PAIR condition (in which a recording of a group yip-howl produced by a male-female coyote pair was the stimulus); and a PACK condition (in which the playback stimulus was a group yip-howl produced by a mixed-sex group of five coyotes). A datalogging receiver at the site of the playback speaker recorded the animals' movements toward or away from the stimulus via the radio-collar transmitter, while a microphone and tape recorder recorded any vocal responses. Responses were compared between the PACK and PAIR conditions to determine whether coyotes perceive differences in group size and adjust their behavior in a manner consistent with game-theoretical models of agonistic behavior.

Coyotes in the central Ohio region were radio-collared as subjects in the field playback experiment. Radio-collaring coyotes was necessary for the field experiments due to their elusive nature, making them an extremely difficult species to observe visually. The collared coyotes were radio-tracked to determine the locations of their home ranges and core territories. This information was needed in planning and interpreting the playback experiment data. In addition, no home range or mortality data on coyotes in Ohio had been published at the time of this study; therefore, the radio-telemetry and mortality data were included as a separate chapter (Chapter 2) of this thesis.

The group-assessment studies described earlier in this chapter focused solely on the target animals' responses during playback experiments in addressing whether the species-specific group territorial vocalizations provided adequate information for assessment of RHP. In the present study acoustic features of the coyote group yip-howl were analyzed to better understand the potential cues contained in the signal that might allow for the perception of group size (Chapter 3). Recordings of group yip-howl choruses used in these analyses were collected from eight captive coyote groups at zoological facilities across the United States.

Finally, the results of the studies discussed in Chapters 2, 3, and 4 are summarized in Chapter 5. Implications of this work and recommendations for future research are also contained in this final chapter.

CHAPTER 2

COYOTE HOME RANGES AND MORTALITY IN AGRICULTURAL-SUBURBAN REGIONS OF CENTRAL OHIO

Introduction

There are few published studies on the home range sizes and ecology of coyotes in the Great Lakes region of the Midwestern United States, which is comprised of the states of Illinois, Indiana, Michigan, Minnesota, Ohio, and Wisconsin (Atwood et al., 2004; Berg and Chesness, 1978; Huegel and Rongstad, 1985; Nelson and Lloyd, 2005). There have also been relatively few studies on coyote home ranges in agricultural and suburban areas in general, although studies of coyote behavior and ecology in these landscapes are increasing in number as coyote population densities increase in these regions.

The study presented here is the first to report coyote home range sizes in agricultural and agricultural-suburban regions of Ohio. Coyotes in this study were radio-collared to allow for monitoring of approach/avoidance movements during field playback experiments (see Chapter 4). Information about home range size and the location of core areas within each animal’s range was necessary for planning and interpreting the results of these experiments. Therefore, the radio-collared coyotes were tracked regularly to determine these spatial areas. When possible, animals were tracked for several weeks before experiments were conducted and for several months following the experiments. The need to obtain the animals' range information for use in experiments conducted during the months of winter and early spring resulted in collection of most location data during these time periods.

Methods

Study Site

Prior to the start of the study in autumn 2003, the researcher contacted the Ohio Division of Wildlife (ODW) seeking contact information for professional nuisance-wildlife trappers who might be willing to assist with coyote trapping for the study. At least two county ODW officers discouraged the researcher from conducting the study in their counties due to the coyote's status with the ODW as a nuisance species and the public's perception of it as a pest. However, the ODW officer in Pickaway County was interested in the study and not only provided the contact information for several trappers in his region, but also offered to do some of the trapping himself. The Pickaway County ODW officer and a nuisance trapper in Pickaway County began trapping for the project in December 2003. In January 2004 a nuisance trapper in Franklin County began trapping for the study. Two additional trappers (a sport trapper and another coyote researcher) in Franklin and Fairfield Counties assisted with the study in 2006. Trappers were not paid for their efforts, serving strictly as volunteers.

The majority of coyotes collared for this study were trapped in Franklin and Pickaway Counties. However, two animals collared during the winter 2006 season were trapped in Fairfield County (Figure 2.1). Some percentage of land in all three of these counties is devoted to agriculture; however, there is also considerable development occurring as well. Pickaway County is still largely agricultural, with 83.9% of its total acreage used for farming. Franklin County is the most developed of the three, with only 25.6% of its total acreage remaining agricultural. Fairfield County falls between these two with 61.2% of its land devoted to farming. (These statistics were obtained from the Ohio Department of Development's website at http://www.odod.state.oh.us).

The topography of the study area consists of a predominantly flat, rolling landscape located northwest of the glacial boundary in Ohio. However, some regions in eastern and southern Fairfield and Pickaway Counties lie on the unglaciated side of the boundary, distinguished by a hillier, more heavily forested landscape.

Central Ohio's climate is characterized by hot, humid summers and cold, dry winters, with the highest temperatures typically occurring in July and the lowest in January. July and January also experience the greatest rainfall and snowfall, respectively. Annual rainfall averages 96.0 cm and annual snowfall averages 70.1 cm. (These statistics are based on climate data for Columbus, Ohio as reported at http://www.usatoday.com/weather/climate/usa/ohio/wcolumbu.htm and http://www.wikipedia.org/wiki/columbus_ohio#climate.)

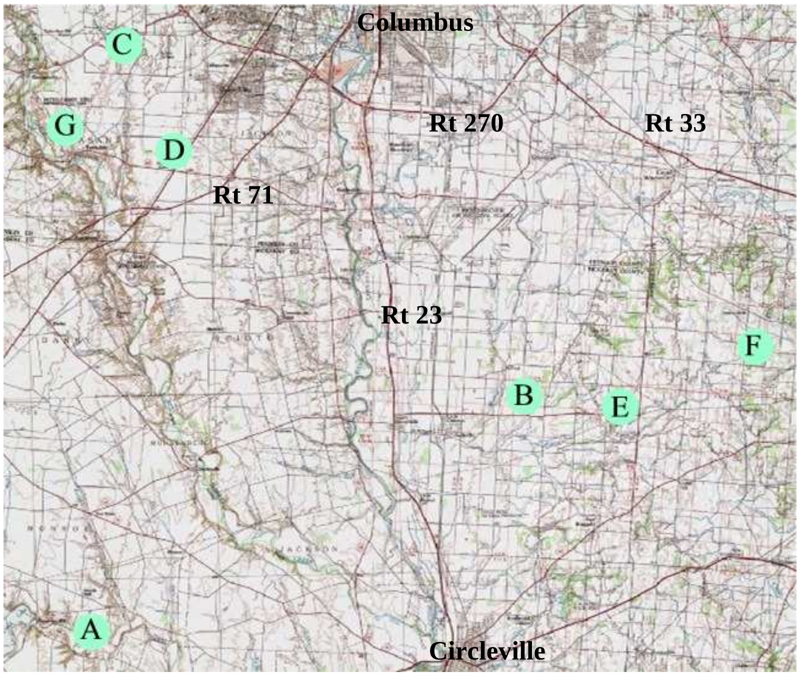


Figure 2.1. Sites in central Ohio where coyotes were trapped, radio-collared and released between 2003 and 2006. A) Williamsport; B) Ashville (west); C) Galloway; D) Grove City (east); E) Ashville (east); F) Greencastle; G) Grove City (west).

Trapping and Radio-collaring

Nineteen coyotes were trapped and radio-collared over three field seasons. Traps were put out from November through March 2003-2004, 2004-2005, and 2005-2006, with no coyotes actually caught until early December. This trapping schedule eliminated the possibility of catching dependent pups.

Our goal was to trap only one animal from any particular social group for the study. Therefore, trapping was conducted in a manner that avoided catching members of the same pack. Some trap sites were used on multiple occasions.

The majority of the coyotes were trapped using 1.75 offset, coil-spring foothold traps, with the staked chain on a center swivel to reduce injury to the animal’s foot.

Three coyotes trapped during the 2005-2006 season were caught using 2.4 mm-diameter cable neck snares equipped with metal stops set at 27 cm to avoid strangulation of the animal. Traps were checked by the trappers, the researcher, or the landowner every 12 hours. When a coyote was found in a trap, the researcher arrived at the trap site within one hour of notification.

Trapped coyotes were restrained with a snare pole (Ketch-All) and chemically immobilized it via an intramuscular lumbodorsal injection of 5:1 ketamine:xylazine at a dosage of 12 mg/kg. Drug induction time was typically just over one minute. Immediately upon complete induction, the trap was removed from the animal’s foot, and the coyote was wrapped in a mylar space blanket and placed on a 61 x 61 cm wooden board covered in foam and burlap. Animals were weighed on this board, which was suspended by chains from a hanging scale (Taylor, model #3311) attached to a modified aluminum camera tripod. After being weighed, the coyote was transferred from the board to the bottom section of a large kennel crate, which was placed inside the researcher’s vehicle in order to prevent the animal from becoming hypothermic in the cold weather. While immobilized, the coyote’s vital signs (pulse, respiration, tissue perfusion, and temperature) were monitored by the researcher while a research assistant tended to any cuts or abrasions the animal suffered on the foot held by the trap, rinsing the wound thoroughly with betadine solution and applying triple antibiotic ointment when necessary. An intramuscular injection of penicillin was also administered in these cases and when any other open cuts or wounds were observed during physical examination. Before rousing from the anesthesia, the animal was examined to determine sex, parasite load, and general physical condition, ear-tagged with one round, plastic, numbered hog tag in each ear (NASCO), and fitted with a 210 g radio collar (Advanced Telemetry Systems, model #M2220B). The ear tags were to serve as a secondary means of identification when animals were reported to have been killed or were found dead, especially if the radio collar had been lost.

The animal's vital signs were monitored throughout the period of chemical immobilization. At the first sign of the animal's recovering from the ketamine effects (e.g., head, tail, or foot movement), a lumbodorsal intramuscular injection of yohimbine was administered to reverse the effects of the xylazine. The top and door of the crate in which the coyote was resting were put in place after the yohimbine administration. The animal was kept in the crate until it appeared to be alert and physically stable, at which time the crate was removed from the vehicle and the coyote released at the trap site. The researcher continued to monitor the animal, following it on foot if necessary, until it moved off normally.

Coyotes typically remained anesthetized for at least 40 minutes under the initial dose of ketamine. However, estrus females roused within 15 minutes after the initial injection, and animals whose body temperatures dropped substantially (by $\geq 15°$ C) were typically unresponsive for longer periods. It was common that an animal would not show signs of complete recovery for over an hour; however, this was not necessarily an effect of the anesthesia. An animal that would withdraw its foot from a toe pinch or show other reflexive signs of recovery in response to tests by the researcher would often remain otherwise immobilized, perhaps from fear.

Radio Telemetry Accuracy Testing

Testing the accuracy of radio telemetry equipment and its users is necessary for interpreting results of studies using telemetry to estimate animal movements and ranges. The researcher conducted accuracy tests during the summer of 2005, testing her accuracy with the handheld telemetry receiver (ATS FieldMaster FM-100), 3-element Yagi antenna, and sighting compass (Suunto KB-14) used to take ground bearings for the study.

Four radio collars that had been or would be deployed in the study were used for testing. One collar was given to each of four landowners with crop farms in the study area. Three farms were located in Franklin County (two in Grove City; one in Galloway), and one farm was in Pickaway County (in Williamsport). Each landowner was asked to place the collar on their property in a location unknown to the researcher. The collars were tied to the tops of 46-cm stakes that were pushed into the ground, leaving the collar positioned approximately 41 cm above the ground’s surface. Upon notification from the landowner that a collar had been placed, the researcher would travel to the property during and between regular radio-tracking sessions to take bearings on the test collar’s position. After determining the general location of the collar during the first visit, three tracking stations were chosen on the property within a range that allowed for strong signal reception. The researcher returned to the property on ten separate occasions to record bearings on a single collar from the three stations, resulting in 30 bearings and 10 location estimates per test collar. Location estimates were calculated using

PalmLocate (Nams, 2005b) on a Palm Zire unit in the field, which was then hot-synched to Locate III (Nams, 2005a) on a personal computer in the lab.

After collecting ten location estimates for a given collar, the researcher homed in on and located the test collar, recording the actual UTM coordinates of the collar's location. The landowner was then asked to place the collar in another location, and the researcher would repeat the telemetry procedure in the new location.

Ten tests were conducted using four radio collars, with two placed three times by the landowners on two of the farms and two placed two times on the other two farms. The individual bearings taken at each station were entered into a Microsoft Excel spreadsheet, and the standard deviation of the ten bearings for each station was calculated to determine the mean standard deviation to be used in determining the error ellipses of animal location estimates in the study. The linear distance between the actual and estimated collar location was also calculated. For each of the ten estimated locations, the differences between the estimated and actual UTM easting and the estimated and actual UTM northing were calculated, providing two distance values in meters. With these values, the linear distance between the estimated and actual test collar location was calculated using the Pythagorean theorem, $a^2 + b^2 = c^2$. In this equation the easting and northing differences were used for values a and b, resulting in the linear distance measurement (c) between the estimated and actual location. The mean linear distance was then calculated from all ten location estimates.

Radio Telemetry

All collars used in this study emitted a beacon signal within the range of 149.5 – 149.9 MHz at a rate of 55 pulses per minute in active mode and 110 pulses per minute in mortality mode. Mortality mode was activated if a collar remained motionless for at least eight hours. The researcher's contact information (name and phone number) was printed on the battery housing of the collar, although it was discovered that this information did not always remain legible when the collar had been deployed for several months.

The annual schedule for radio tracking was divided into three seasons: breeding/gestation (January through April); pup-rearing (May through August); and dispersal (September through December). These seasonal delineations were based on those described in Gese et al. (1988) and Grinder and Krausman (2001). Since field playback experiments with the collared animals were conducted during late winter and early spring, the animals' home ranges during the breeding/gestation season were of greatest interest. Therefore, most location data were collected during that season.

On average, radio-collared coyotes were located 2.6 times per week during breeding/gestation season, 1.1 times per week during pup-rearing season, and once every 3 weeks during dispersal season. However, since new animals were collared each December, animals were typically tracked 1.4 times per week during that month of the dispersal season. Animals were tracked both during the day and at night. Diurnal locations were those taken between the hours of 07:30 and 19:29; nocturnal locations were those between the hours of 19:30 and 07:29. Consecutive locations on an animal were not included in analyses if the locations were collected within 8 hours of each other.

The radio-tracking methods changed over the three years of the study. During the first field season (2003-2004) all tracking was done from the road using an ATS FM-100 receiver, a handheld 3-element Yagi attenna, and Telex headphones. This method required that the researcher get out of the vehicle every mile or so when within what was believed to be the range of a radio-collared coyote and listen for that animal's beacon signal. This was especially challenging when tracking transient or dispersing individuals, who would often travel long distances over short time periods in an unpredictable manner. When a strong radio signal was received, the researcher used the method of bisecting the nulls to determine the direction of the animal and took a bearing using the sighting compass. Two or three bearings were taken within a 10-minute period in order to estimate the location of the coyote.

An improvement was made to vehicle-based tracking for the 2004-2005 field season. An antenna mount was custom built for the top of the vehicle. This mounting apparatus held a 4-element Yagi antenna, which was connected via an 8-ft cable to a receiver (LOTEK model SRX400A) inside the vehicle. Although the antenna did not rotate, this setup allowed the researcher to listen for collar beacon signals from within the vehicle while driving through areas in which study animals might be located. When a strong radio signal was picked up from a collar, the researcher would use the handheld system to take bearings from outside the vehicle, as described above. This method of vehicle-based tracking was continued through the end of the study.

Coyotes were periodically located from the air during the 2005-2006 field season using the Ohio Division of Wildlife's (ODW) fixed-wing aircraft (Partenavia P68C).

Since ODW did not have a receiver tuned to the 149 MHz range being used in the study, the researcher flew with the pilot, using the LOTEK receiver to pick up radio-collar beacons. When a strong signal was heard, the Event-Log function of the receiver was turned on and the gain turned down to best determine the location of the collared animal. Event-Log displays the signal strength from the transmitter on the LED screen of the receiver, with a maximum strength of 232 units. When a signal was near or at maximum strength, the pilot would tightly circle the area to confirm the location, and GPS coordinates were recorded by the researcher. In September 2005, three animals from the previous field season that had gone missing in winter and spring 2005 were located. The airplane-based telemetry was invaluable during the 2005-2006 field season in locating wide-ranging animals.

Data Analyses

Telemetry data collected during the first two field seasons (2003-2004 and 2004-2005) were manually recorded on data sheets in the field, and later entered into Locate II (Nams, 1990). Coyote locations were triangulated with Locate and recorded in Universal Transverse Mercator (UTM) units. Bearing data were considered usable if they resulted in an estimated location, using the Maximum Likelihood Estimator (MLE) in Locate II.

During summer 2005 the researcher beta tested new Windows and PDA versions of the Locate program (Locate III and PalmLocate, respectively) being developed for data management in the field. This testing proved both packages provided improved methods of data collection and entry; therefore, Locate III and PalmLocate were the location-estimate programs used throughout the end of the project.

Locations were plotted on digital UTM maps and home ranges were estimated using ArcView GIS 3.2. The maps used in ArcView were TIFF files exported from National Geographic's Ohio TOPO! map software. Each exported TOPO! map was georeferenced for ArcView by creating associated world files (.TFW files) based on the map's corner coordinates and its image size in pixels. The X and Y pixel sizes for world files were calculated by dividing the map's left-to-right and top-to-bottom distances (in meters) by the map's image width and height (in pixels), respectively. Rotation terms in all world files were set to zero.

Home ranges were calculated using the fixed kernel analysis function in the Animal Movement Extension for ArcView (Hooge and Eichenlaub, 2000). The least squares cross validation (LSCV) of the smoothing factor was used to determine the parameter that provided the lowest mean integrated squared error for the kernel density estimate. The developers of the Animal Movement extension argue that the ad hoc default setting for the LSCV provides an estimator that is less biased than alternative smoothing factor values selected by the user (Hooge and Eichenlaub, 2000). Both 95% and 50% utilization distributions (UD) were calculated, with the 95% UD estimating an animal's total home range for a given time period, and the 50% UD estimating the core area of the home range for that same period. Seasonal and annual home ranges were calculated for individuals for which 30 or more locations had been collected during the time period of interest. This decision was based on Seaman et al.'s (1999) recommendation that a minimum sample size of 30 locations be used when analyzing home ranges with kernel estimators.

Survival probabilities for the radio-collared coyotes in the study were calculated using the staggered-entry design of the Kaplan-Meier survival estimator described by Pollock et al. (1989). This design allows for the addition of tagged animals into the survival estimate over time. It also allows for the inclusion of animals of unknown fate by “censoring” these animals in the analysis. Censoring resulted in the subtraction of the missing animal from the number of individuals considered at risk at the next time point after the animal had disappeared.

Results

Study Animals

Nineteen coyotes were radio-collared during the 3-year study, 9 males and 10 females. Although coyotes were trapped, collared, and released within a roughly 1,600 km^2 region, dispersing and transient animals often ranged far beyond this area, and in some cases, beyond the counties in which they were trapped. Overall, the study animals ranged within nine central Ohio counties, covering an approximately 11,500 km^2 area, as shown in Figure 2.2. Table 2.1 provides general information about the study animals.

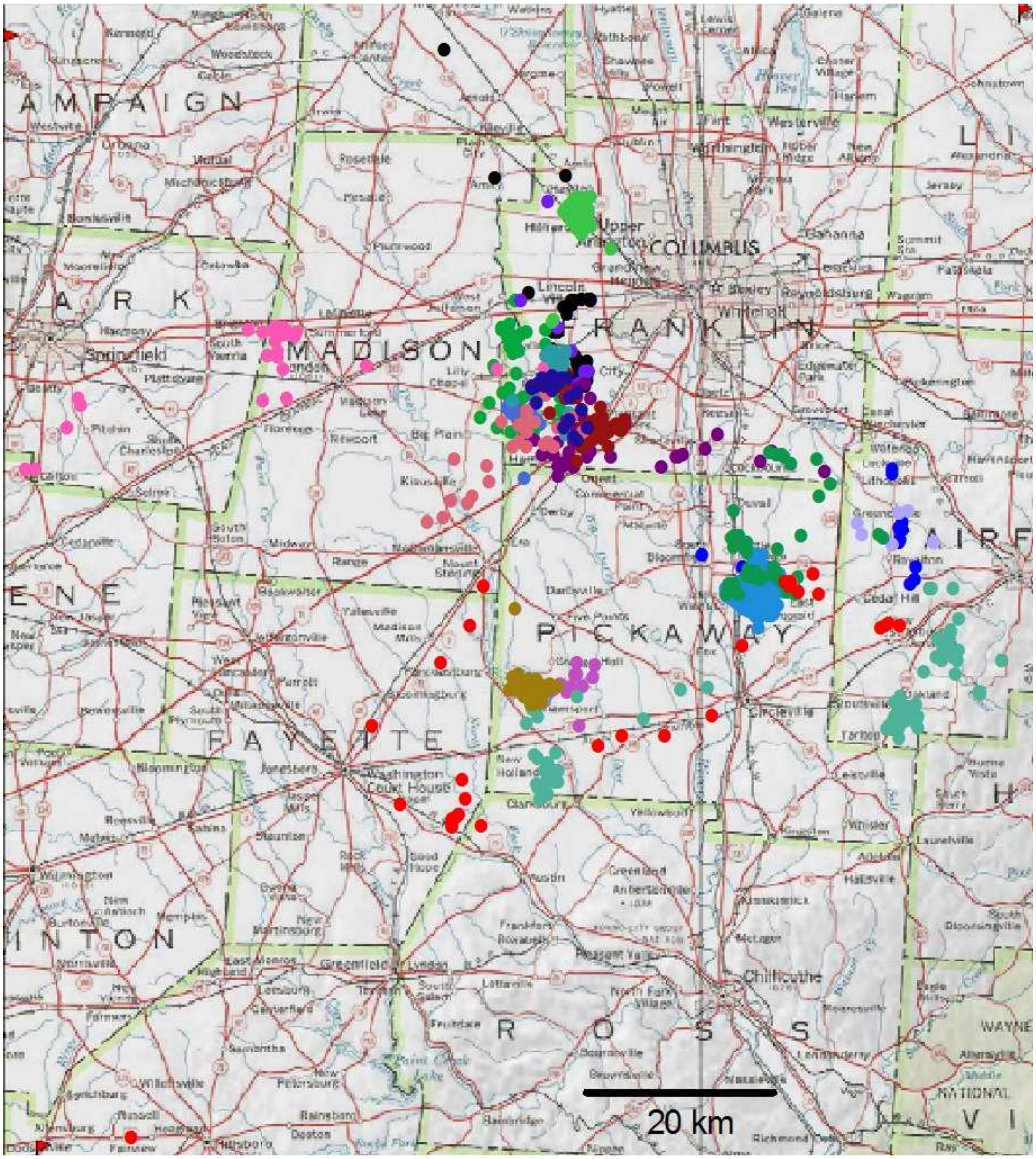


Figure 2.2. All locations of the 19 radio-collared coyotes during the study period. Colored dots represent individual location estimates; each radio-collared coyote is represented by a different color. (Mapped area represents region of central Ohio west and south of Columbus, Franklin County.)

ID	*Weight (kg)*	*Date Collared*	*Trap Site*	*Last Date Located*	*Total No. Locations*	*Status at End of Study**
M501	19.1	12/8/05	Ashville, PC	1/16/06	14	D
F502	12.3	3/1/06	Grove City, FrC	10/3/06	43	D
F524	11.3	12/18/04	Galloway, FrC	11/28/05	50	D
F543	12.7	12/20/03	Williamsport, PC	2/24/04	37	M
F564	13.6	1/14/04	Galloway, FrC	11/13/04	65	D
M582	13.6	12/23/03	Ashville, PC	10/5/06	192	C
M603	13.2	1/11/06	Galloway, FrC	2/13/06	10	M
F621	11.3	1/21/06	Greencastle, FaC	2/4/06	8	D
M643	16.3	2/9/04	Grove City, FrC	6/13/04	50	D
F644	14.5	2/10/06	Greencastle, FaC	10/5/06	52	D
M663	18.1	1/6/05	Galloway, FrC	2/13/06	44	D
M682	17.2	1/26/04	Ashville, PC	3/6/04	31	D
M703	15.0	12/24/05	Galloway, FrC	10/3/06	68	C
F722	†12.3	12/23/04	Williamsport, PC	10/5/06	126	C
M742	15.9	2/10/05	Williamsport, PC	12/26/05	72	D
F763	17.2	3/6/05	Grove City, FrC	1/30/06	69	D
F782	12.7	12/13/05	Galloway, FrC	10/3/06	71	C
M812	18.1	2/18/06	Grove City, FrC	4/21/06	27	D
F831	14.5	2/14/06	Grove City, FrC	4/1/06	25	D

* D = deceased; M = Missing/Unknown Fate; C = Current/On Air
† Weight estimated.

Table 2.1. General information on radio-collared coyotes.

Although coyotes were not aged by tooth eruption or wear, other indicators of adulthood were observed in five of the animals, 2 males and 3 females. The dental and general physical condition of two males (M582 and M812) suggested they were adult animals. Coyote M582 had yellow-stained teeth, a number of small scars on his body, and only 2/3 of his tail. In addition, he was visually observed with another coyote (presumably his mate) and at least two pups in June 2004. This coyote also remained in the same home range for all three years of the study. Coyote M812 had three broken canines and his coat was in very bad condition. Two canine teeth of one female (F831) were also broken. This same female did not appear to be in general good health, most likely due to having been shot prior to collaring, as evidenced by healing buckshot wounds observed in the caudal region of her body. One female (F763) had elongated, darkened nipples, indicating that she had previously nursed a litter (Mech et al. 1993). The third female (F722) may have been a yearling when collared in December 2004, but she survived through 2005 and 2006. Therefore, she was known to be an adult during the last field season of the study.

Three females were believed to be in estrus at the time of collaring. One female (F644) was observed to be in estrus while being examined during the collaring procedure. Two other females (F564 and F524) were also believed to be in their estrus cycle due to their failure to remain immobilized during the ketamine knock-down. These females roused from the knock-down within 10 – 15 minutes of the initial ketamine injection, a common response in estrus females (Dr. Thomas Klein, DVM, personal communication, January 26, 2004).

All animals, except one female (F722), were weighed during the collaring procedure. An independent samples T-test showed that male coyotes weighed significantly more than females ($p = .003$), with male weights averaging 16.28 ± 2.06 kg ($N=9$) and female weights averaging 13.24 ± 1.79 kg ($N = 10$). The weight difference is still significant ($p = .006$) when the estimated weight for F722 is excluded from the analysis.

Radio Telemetry Accuracy Testing

The mean standard deviation of the 30 sets of bearings taken during accuracy testing of the telemetry system was 5.86°. This value was used as the fixed bearing standard deviation in Locate III for estimating all error ellipses for animal location estimates. The mean linear distance between estimated and actual test collar locations in the accuracy tests was 105 m. The range of calculated linear distances was 36 – 248 m, with a median of 68 m.

The mean standard deviation and mean linear distance values determined by this accuracy test were acceptable for the purposes of this study. The objective of the study was to estimate the radio-collared coyotes' home ranges to aid in planning and interpretation of field playback experiments conducted with the animals. Such estimates do not require the fine grain resolution needed for studies of animal movement or habitat use.

Classification of Radio-Collared Coyotes

The radio-collared coyotes were classified as residents, transients, dispersers, or settlers based on their movements during the study period. Animals whose movements occurred within a predictable area, making them easily locatable, were considered residents. Animals whose movements were unpredictable and who were difficult to locate during tracking sessions were labeled transients. Dispersers were those animals that moved in a predictable manner within an area for some time, but then whose movements became unpredictable and led them away from their original "home" area. Settlers were defined by movement patterns opposite those of dispersers: they ranged in an unpredictable manner, but then settled as an apparent resident in a new location.

Five of the nineteen radio-collared animals were not classified due to insufficient location data (i.e., < 2.3 months of tracking data). Two additional animals also were collared for very short time periods (< 2 months), but their status could be inferred, even with limited data.

To quantify the general movement of the animals that led to their classification as resident, transient, etc., the mean distance between pairs of consecutive locations was calculated for each radio-collared coyote. Prior to performing this calculation, the average time intervals between locations for all animals were equalized by removing location estimates collected at outlier intervals (i.e., intervals that were unusually short or long). These adjustments to the data set resulted in the average numbers of locations per month given in Table 2.2, which were used to compute the mean distances between locations for each animal (shown in Figures 2.3, 2.4, 2.5, and 2.8). Home-range analyses, described in the following section, further elucidate each animal's ranging status.

Month	Mean Days Between Locations	Month	Mean Days Between Locations
Jan	3	Jul	14
Feb	2	Aug	22
Mar	2	Sep	21
Apr	4	Oct	22
May	6	Nov	43
Jun	6	Dec	6

Table 2.2. Mean number of days between consecutive location estimates by month.

Animals believed to be residents could be divided into two categories: small-range and wide-ranging residents (Figures 2.3 and 2.4). The overall mean distance between consecutive locations for small-range residents was 1.84 ± 1.53 km (N = 313), with the means for individual animals ranging from 0.97 to 2.28 km. Five animals, three females and two males, were classified as small-range residents. Two female coyotes were classified as wide-ranging residents, with mean distances between locations of 4.17 ± 3.06 km (N = 48) and 2.98 ± 2.99 km (N = 42). The location data for two of the small-range coyotes, F502 and F782, suggest they were resident animals during most of the study period, but were possibly beginning to make dispersal movements when the study ended at the beginning of the 2006 dispersal season (Figure 2.3a & d).

Two male coyotes, M603 and M682, for whom there were only 1.1 and 1.3 months of tracking data, respectively, were classified as transients. The mean distance between locations for M603 was 6.21 ± 5.38 km (N = 8) and for M682 was 5.47 ± 4.73 km (N = 23). It is possible that one or both of these animals was in the process of dispersing from its natal site, but that could not be confirmed from the data available. However, it was evident from the data that they moved great distances over short periods of time. Coyote M603 could not be located by ground or air after 13 February 2006. Animal M682 was killed on 17 March 2004 more than 90 km southwest of his trap site.

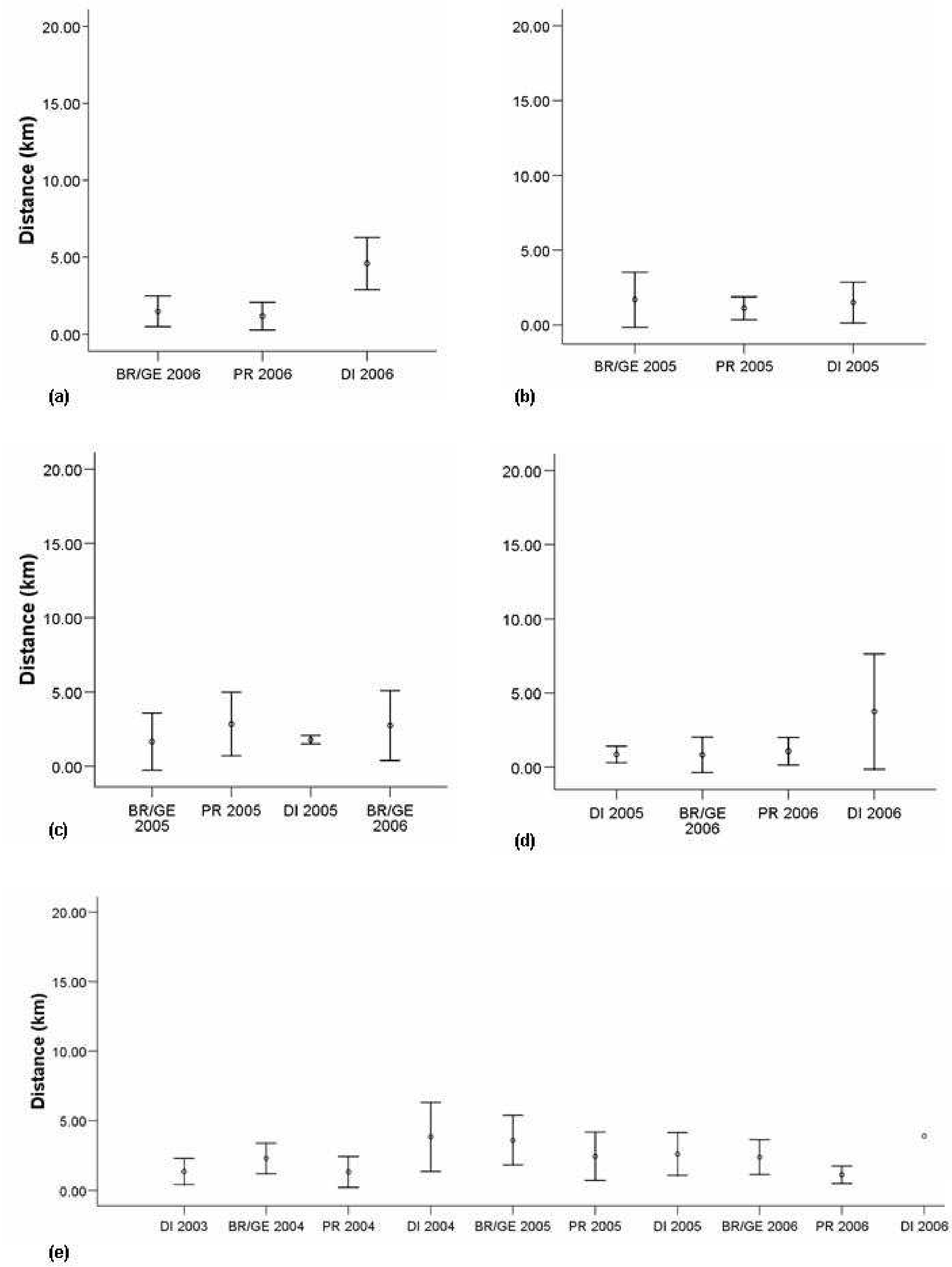


Figure 2.3. Mean distances between consecutive locations for small-range resident coyotes: a) F502, b) M742, c) F763, d) F782, and e) M582. X axis represents season (BR/GE = breeding/gestation; PR = pup-rearing; DI = dispersal).

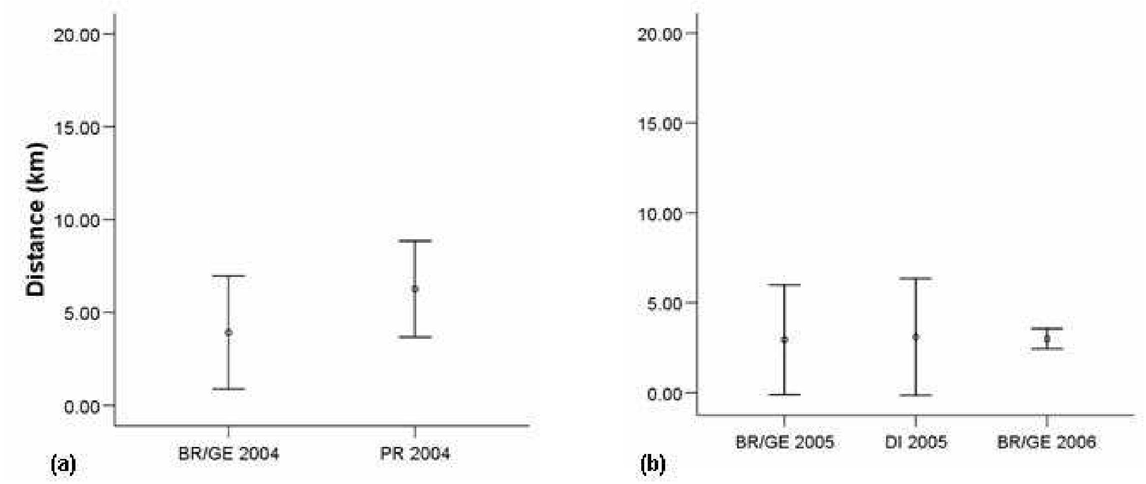


Figure 2.4. Mean distances between consecutive locations for wide-ranging resident coyotes: a) F564 and b) F644. X axis represents season (BR/GE = breeding/gestation; PR = pup-rearing; DI = dispersal).

To definitively classify a coyote as a natal disperser, the animal would have to be tagged and tracked from birth. That was not the case with any of the animals in this study. However, two coyotes (F524 and M643) who appeared to be younger animals displayed a pattern of movement associated with dispersal movements in some mammal species, including coyotes (DeStefano et al., 2006; Gese et al., 1996; Harrison et al., 1991; Kamler et al., 2004). Both animals were found in a fairly well-defined range, in which they moved predictably, for a period of time after being collared. However, at some point, each animal began taking excursions from its original range, and eventually did not return (Figure 2.5).

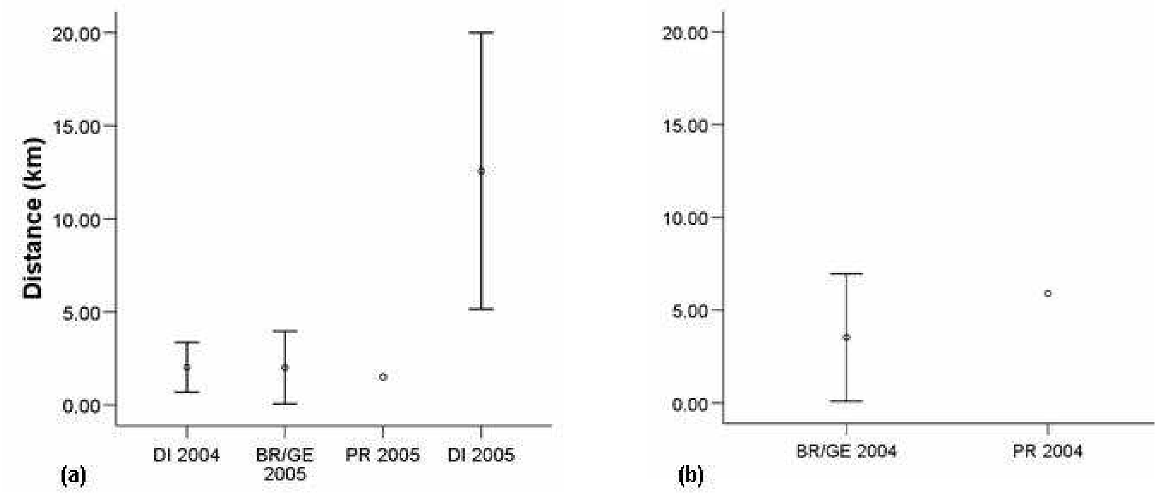


Figure 2.5. Mean distances between consecutive locations for dispersing coyotes: a) F524 and b) M643. X axis shows seasonal data (BR/GE = breeding/gestation; PR = pup-rearing; DI = dispersal).

From mid-December 2004 through mid-February 2005, F524's mean distance between locations was 1.56 ± 0.95 km. On 11 Feb 2005 she was located 5.3 km from her "home" area, but then was found "home" again the next day (Figure 2.6). She continued making these excursions out and back through 21 March 2005, always traveling north of her "home" area. She was located in one of these excursion areas, approximately 7.5 km from "home" on 26 March 2005 and was never found in the "home" area again. However, the mean distance between her locations from mid-February through early-May 2005 was only 2.75 km, similar to the wide-ranging residents described above. This coyote could not be located again after 9 May 2005 until tracking by air began in late September. On 26 September, she was located almost 15 km from her last location site. She continued ranging great distances over short time periods until she was killed on 10 December 2005.

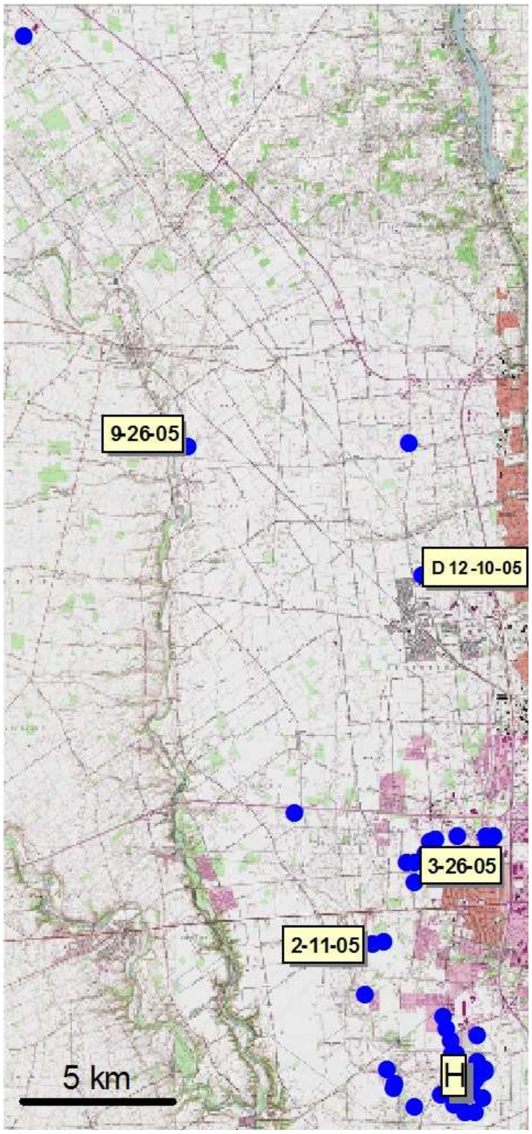


Figure 2.6. Locations of coyote F524, assumed to have been dispersing during study period. Map shows original "home" site (H), plus locations at other dates referred to in text. Blue dots represent all location estimates collected for this radio-collared coyote. (Mapped area represents region immediately west of Columbus, Franklin County, OH.)

The movement pattern of coyote M643 was similar to that of F524. The original range in which he was found was larger and less well-defined than that of F524, with a mean distance between locations of 2.8 km. He was located in this area from 9 February

2004, when he was collared, to 14 April 2004, at which time he was located approximately 5 km east of his “home” area (Figure 2.7). He was located at “home” on 26 April, where he was found through early May. However, on 21 May he was found approximately 23 km east of the “home” area. He was found only east of the “home” area from this date through 20 July 2004, when he was killed.

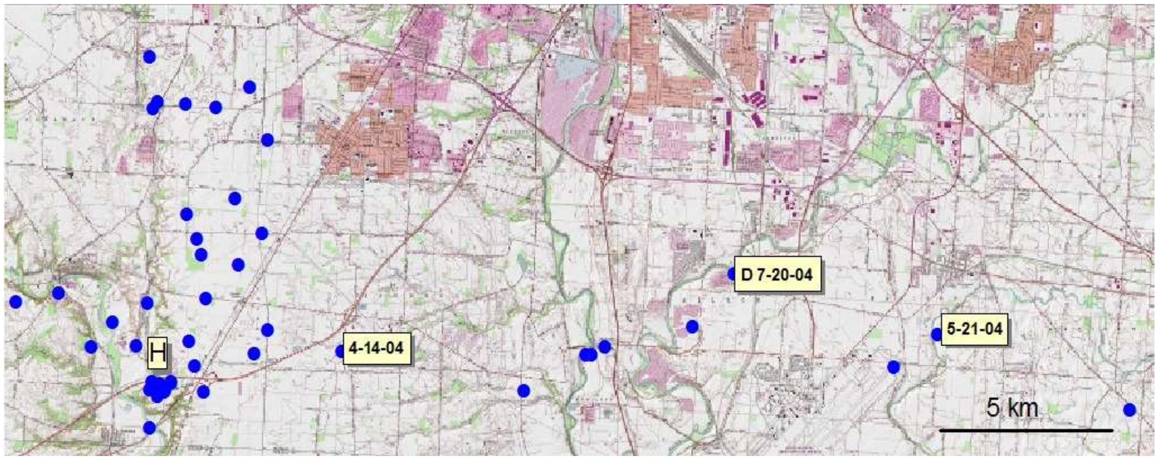


Figure 2.7. Locations of coyote M643, assumed to have been dispersing during study period. Map shows original “home” site (H), plus locations at other dates referred to in text. Blue dots represent all location estimates collected for this radio-collared coyote. (Mapped area represents region immediately southwest of Columbus, Franklin County, OH.)

The three remaining coyotes (M663, M703 and F722) for which sufficient location data were available displayed “settlement” behavior (Figure 2.8). The two male coyotes ranged in a manner similar to transients or dispersing animals immediately after being collared. From 6 January 2005, when he was collared, through 5 February 2005, the mean distance between locations for M663 was 7.6 km. By the end of this period he had traveled more than 56 km ESE from the trap site (Figure 2.9). This coyote was not located again until air tracking commenced in late September, at which time he was located approximately halfway between the trap site and his furthest known location. From 26 September 2005 when he was re-located through 16 February 2006, when he was killed, he remained in this new range and the mean distance between his locations was 1.2 ± 1.04 km.

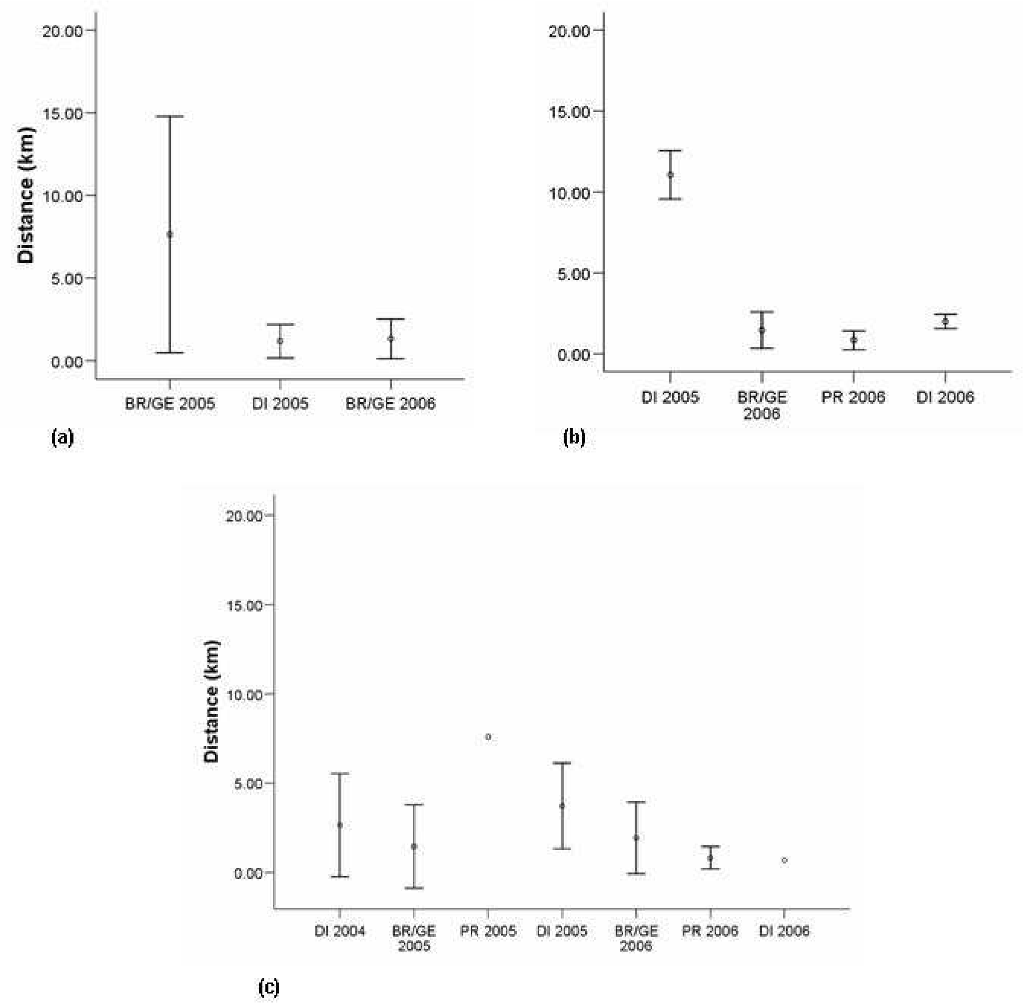


Figure 2.8. Mean distances between consecutive locations for coyotes classified as settlers: a) M663, b) M703, and c) F722. X axis shows seasonal data (BR/GE = breeding/gestation; PR = pup-rearing; DI = dispersal).

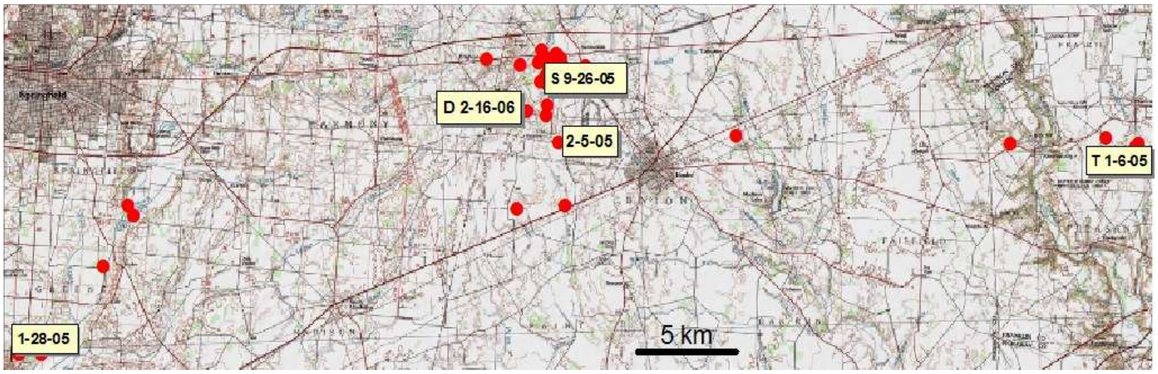


Figure 2.9. Locations of coyote M663, assumed to have been transient and settled into a small range during study period. Map shows trap site (T 1-6-05) and site of settlement (S 9-26-05), plus locations at other dates referred to in text. Red dots represent all location estimates collected for this radio-collared coyote. (Mapped area represents region west of Columbus, including Franklin, Madison, and Clark Counties, OH.)

Coyote M703’s mean distance between locations was 7.1 km from the date he was collared (24 Dec 2005) through 5 January 2006, when he “settled” in an area approximately 20 km NW of the trap site (Figure 2.10). From this time until the end of the study’s tracking period (3 October 2006) and beyond, he remained in this new range. The mean distance between his locations in this new area was 1.3 (± 1.0 S.D) km.

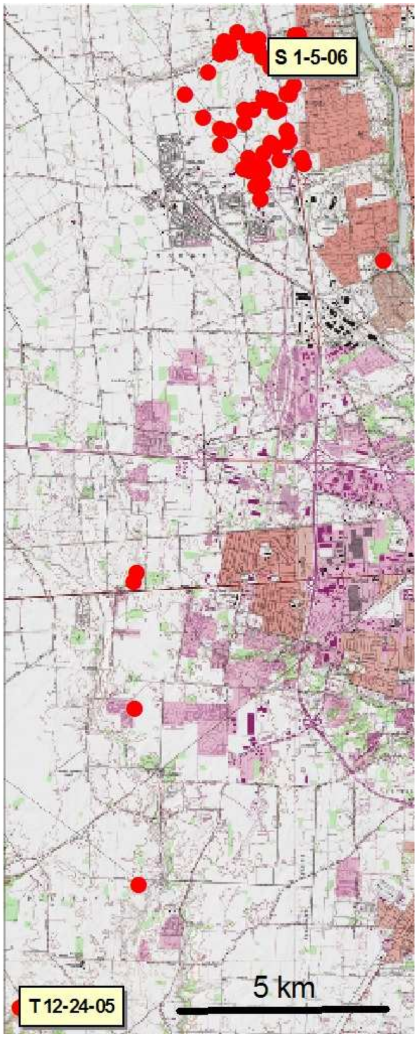


Figure 2.10. Locations of coyote M703, assumed to have been transient and settled into a small range during study period. Map shows trap site (T 12-24-05) and site of settlement (S 1-5-06). Red dots represent all location estimates collected for this radio-collared coyote. (Mapped area represents region immediately west of Columbus, Franklin County, OH.)

The location data for female coyote F722 suggest that she might have dispersed from her natal group about three months after being collared and then settled in a region over 35 km away (Figure 2.11). During the first three months, from 23 December 2004 through 11 March 2005, she remained in a fairly well-defined area, with the mean distance between locations being 1.2 (± 2.4 S.D) km. As with the dispersers described above, she made at least one excursion in the direction in which she ultimately moved and returned to the original home area before leaving permanently. From that first excursion in mid-March through 16 May 2005, the mean distance between her locations was 6.5 ± 5.5 km. She could not be located by vehicle tracking after 16 May, but she was re-located on 26 September 2005 by air 23 km from her last known location. She ranged in a wide but predictable manner in this new area, with the mean distance between her locations being 3.3 ± 2.8 km. However, on 15 Feb 2006 she was found approximately 11 km SW of this new primary range, and she remained in this new area through the end of the study's tracking period in October 2006 and beyond. The mean distance between her locations in this new range was 1.2 ± 0.72 km. In addition, her fidelity to one particular wooded area in the region suggested that she might have mated and produced a litter during the 2006 breeding season.

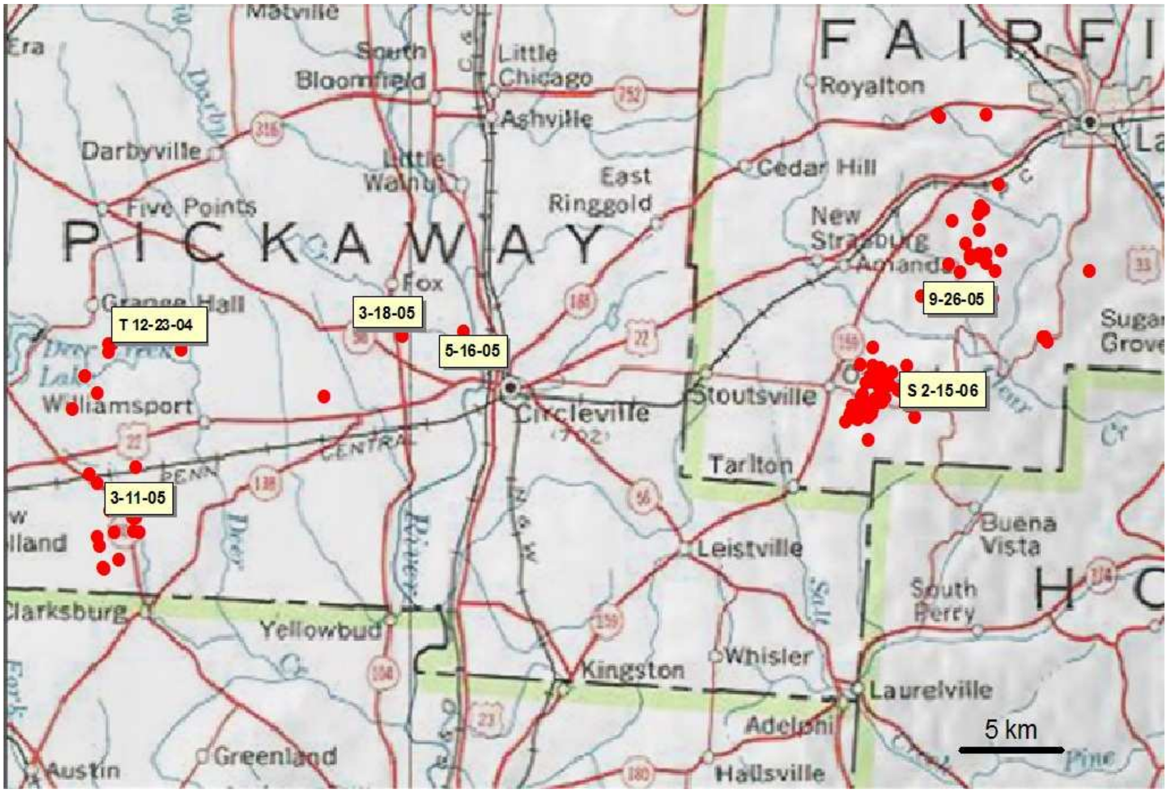


Figure 2.11. Locations of coyote F722, assumed to have dispersed and settled into a small range during study period. Map shows trap site (T 12-23-04) and site of settlement (S 2-15-06). Red dots represent all location estimates collected for this radio-collared coyote. (Mapped area represents region of central Ohio, including portions of Fairfield, Hocking, Pickaway, and Ross Counties.)

Home Range Estimates

Over the three years of the study, 1,054 usable locations were taken on the nineteen radio-collared coyotes. The number of locations per animal ranged from eight, on a coyote that was killed two weeks after being collared, to 192, on an animal that survived the entire three years of the study. Overall, 55.6% of the total number of locations were taken during daytime hours (07:30 – 19:29), with 44.4% taken at night (19:30 – 07:29).

A sufficient number of locations (≥30) for either seasonal or annual home range estimation were available for 14 of the 19 radio-collared animals. Table 2.3 displays the home range estimates calculated for these animals, broken down by 95% and 50% UDs for both seasonal (breeding/gestation period) and annual data sets.

	Seasonal Home Range Estimates (km^2)						***Annual Home Range Estimates (km^2)***					
	BR/GE 2004		BR/GE 2005		BR/GE 2006		2004		2005		2006	
ID	95%	(50%)	95%	(50%)	95%	(50%)	95%	(50%)	95%	(50%)	95%	(50%)
Small-Range Residents:												
F502											14.9	(2.6)
M582	25.0	(4.2)			23.0	(1.2)	24.7	(3.5)	21.3	(1.3)	19.2	(1.0)
M742			13.1	(2.6)					13.0	(2.6)		
F763									20.3	(3.1)		
F782					2.3	(0.5)					3.1	(0.9)
Wide-Ranging Residents:												
F564	140.5	(18.1)					131.6	(17.1)				
F644					159.5	(24.7)					145.2	(28.9)
Transients:												
M682	2071.6	(334.4)										
Dispersers:												
F524			44.0	(6.5)								
M643	79.2	(6.3)					151.4	(16.6)				
Settlers:												
M663											4.7	(0.5)
M703					11.8	(1.9)					10.7	(0.7)
F722			18.3	(3.2)	51.7	(6.6)			398.6	(74.0)	33.8	(5.0)

Table 2.3. Breeding/Gestation (BR/GE) season and annual home range estimates (95% and 50% utilization distributions) for fourteen coyotes radio-collared in central Ohio from December 2003 through March 2006. (Annual 2006 home range estimate for coyote 663 (shaded cells) was calculated using location data for the period September 26, 2005 through February 16, 2006, at which time the animal was killed.)

Annual 95% UD home range estimates for small-range residents ranged from 3.1 to 24.7 km^2. The 2006 annual home ranges of two of the three settlers also fell within this range. Although the 2006 annual home range of F722 was larger than 24.7 km^2, it is closer in size to the home range estimates of the small-range residents than those of the wide-ranging residents. Also, the annual estimate includes F722’s movements prior to her “final” settlement in February 2006. Her final range was substantially smaller and fell within the range of the small-range residents.

Annual diurnal and nocturnal home range estimates were also calculated for all resident coyotes, using data from the first year for which the animal was known to be a resident. Both 95% and 50% UD estimates were computed. The results of Wilcoxon signed-rank tests comparing diurnal and nocturnal range sizes within either the 95% UD or the 50% UD for the seven resident animals (small-range and wide-ranging) were non-significant (95% UD: $T+ = 5$, $N = 7$, $p = 0.31$; 50% UD: $T+ = 5$, $N = 7$, $p = 0.80$). Similar comparisons of this data for the five small-range residents only were also non-significant (Wilcoxon signed-rank test, 95% UD: $T+ = 4$, $N = 5$, $p = 0.14$; 50% UD: $T+ = 4$, $N = 5$, $p = 0.41$). The non-significant results from the five small-range resident coyotes’ data is largely due to the range-size pattern for coyote M582 in 2004. In that year, the first year for which M582 was collared and known to be a resident, his diurnal range was larger than his nocturnal range for both the 95% and 50% UDs. This pattern was opposite that of the other four residents’ ranges, in which the nocturnal range was larger than the diurnal. When the signed-rank test was performed using M582’s 2005 or 2006 data, the difference between diurnal and nocturnal range size for the small-range residents was significant for both the 95% and 50% UDs, with $p = 0.04$ for both range sizes in both years. Using these years’ data, instead of M582’s 2004 data, all nocturnal ranges were larger than diurnal ranges, with a consistently greater difference between them for the 50% UD (Figure 2.12).

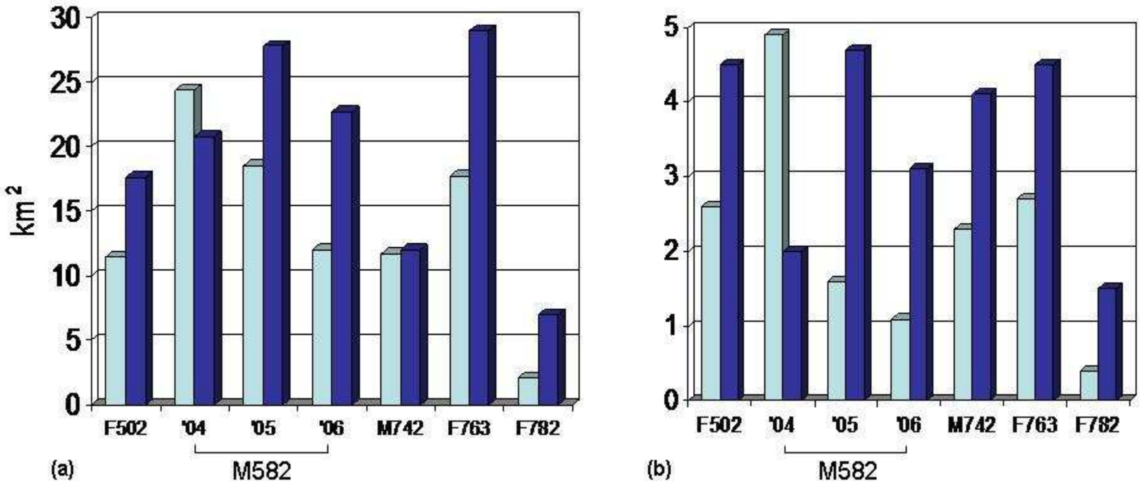


Figure 2.12. Diurnal and nocturnal kernel home range estimates for small-range resident coyotes (diurnal: light-blue bars; nocturnal: dark-blue bars): a) 95% UD estimates, b) 50% UD estimates. Coyote IDs are shown on X axis.

Maps of the diurnal and nocturnal ranges indicate another common pattern. Figure 2.13 shows maps of the small-range residents' ranges, plus the final ranges of the two animals that were transient and then settled in a small range. With the exception once again of M582's 2004 UD estimates, the diurnal core area (50% UD) for each animal not only fell within the nocturnal 95% UD but consistently overlapped with, or more regularly was contained within, the nocturnal 50% UD.

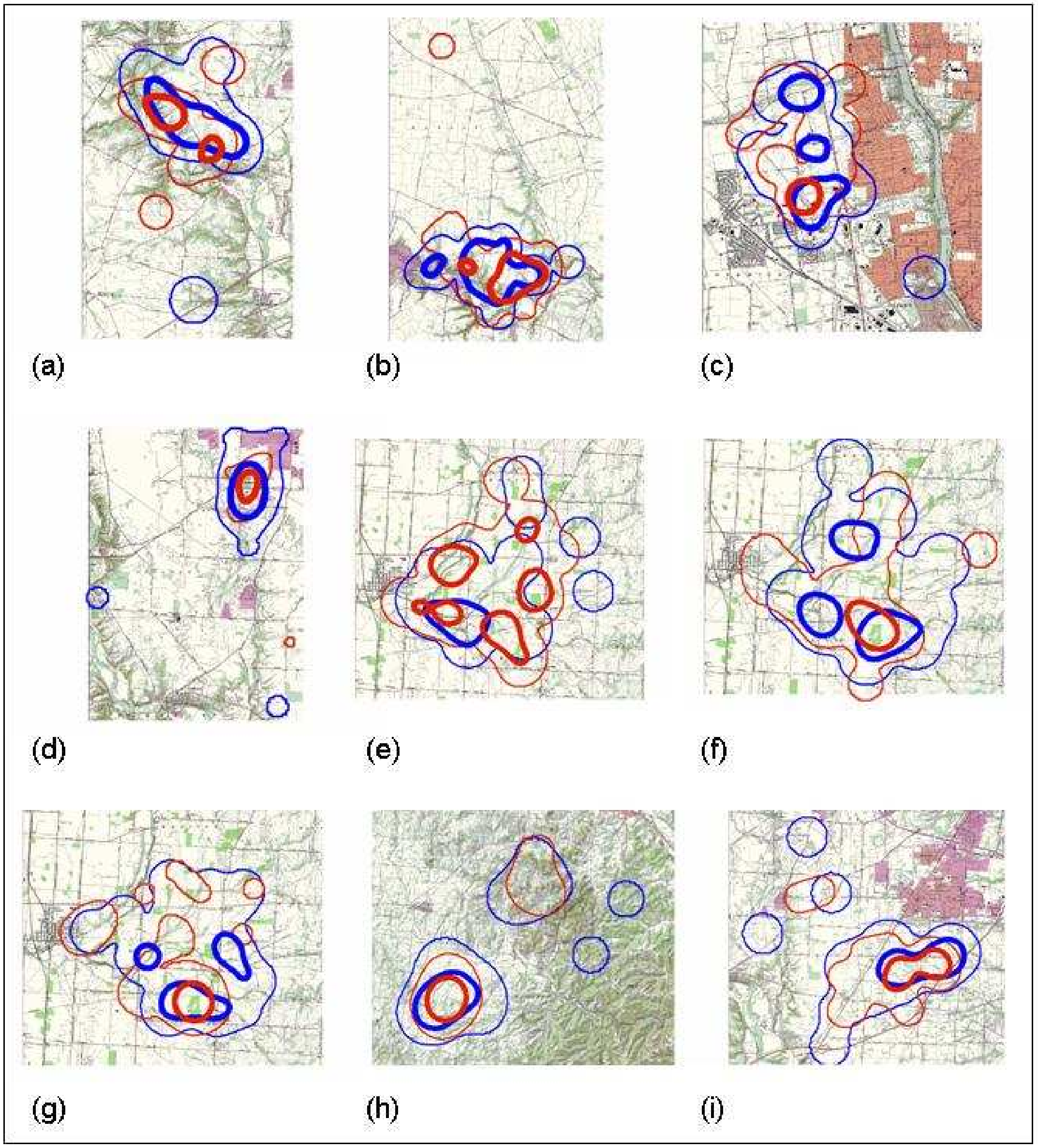


Figure 2.13. Annual home range maps for small-range resident coyotes and animals that settled into small ranges, indicating 95% (thin outlines) and 50% (thick outlines) UD kernel estimates for diurnal (red) and nocturnal (blue) ranges. Maps represent ranges for a) F502, b) M742, c) M703, d) F782, e) M582 (2004), f) M582 (2005), g) M582 (2006), h) F722, and i) F763.

Mortality

Of the 19 coyotes radio-collared, only four were confirmed alive at the end of the three-year study. As shown in Table 2.4, ten of the coyotes were known to have been shot or trapped. Although coyote F564 is categorized as “unknown fate,” she was most likely shot during deer hunting season, as her radio-collar was found the week following deer gun season near an abandoned rural property. The transient male M682 was found by a landowner hanging by a broken rear leg in a barbed-wire fence. The animal was barely alive when discovered and was subsequently shot by the landowner. Although categorized as “mortality (other),” coyote F831’s death was also apparently human-induced. During the collaring procedure, it was observed that she had recently been shot, with buckshot wounds apparent on the caudal region of her body. She was found dead by a landowner 1.5 months later, apparently having died from a systemic infection.

The fate of two of the study animals remains unknown. Coyote F543 could not be located just over two months after having been collared. It is possible that she dispersed from the region where she had been located. When aerial tracking commenced in September 2005, we attempted to locate F543 but were unsuccessful. Although M603 was moving over great distances immediately after being collared, we were surprised that he could not be located via aerial tracking. The pilot and researcher searched extensively throughout central Ohio on a number of occasions, but never re-located this animal.

ID	Months Collared	Human-Induced Mortality			Unknown Fate	Known to be Alive Oct 2006
		Shot	Trapped	Other		
M501	1.30		X			
F502	7.20	X				
F524	11.50		X			
F543	2.20				X	
F564	10.13				X	
M582	33.90					X
M603	1.10				X	
F621	0.47		X			
M643	4.17	X				
F644	7.90	X				
M663	13.43	X				
M682	1.33			X		
M703	9.43					X
F722	21.70					X
M742	10.63	X				
F763	11.00		X			
F782	9.80					X
M812	2.07	X				
F831	1.53			X		

Table 2.4. Fate of 19 radio-collared coyotes in 3-year study.

Long-term survival of the 19 radio-collared coyotes over 37 months (from January 2004 to January 2006) was 0.04 (Figure 2.14). Annual survival for each year of the study varied, with the probabilities for 2004, 2005, and 2006 calculated as 0.25, 0.67, and 0.23, respectively (Figure 2.15). Chi-square analyses comparing the survival probabilities between the years were all non-significant (2004-2005: $\chi^2 = 2.10$, df = 1, p = 0.17; 2004-2006: $\chi^2 = 0.06$, df = 1, p = 0.83; 2005-2006: $\chi^2 = 2.74$, df = 1, p = 0.10).

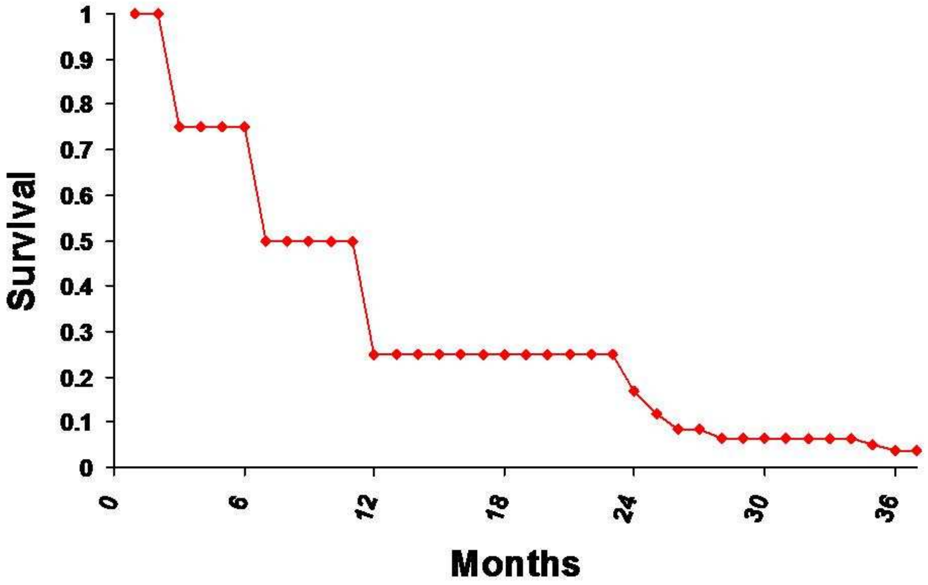


Figure 2.14. Kaplan-Meier staggered entry survival functions of 19 radio-collared coyotes for period January 2004 to January 2006.

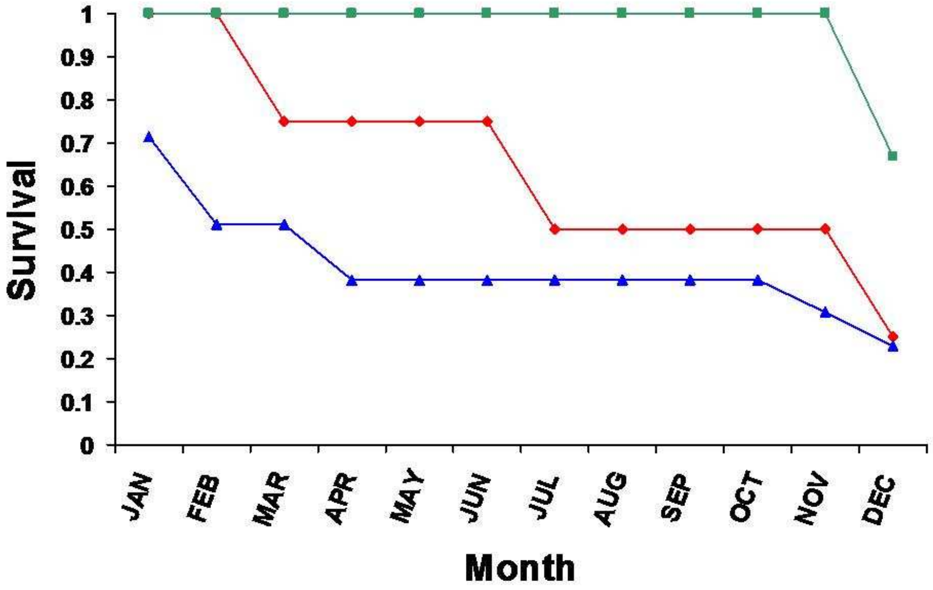


Figure 2.15. Kaplan-Meier staggered entry survival functions of 19 radio-collared coyotes during 3 years of study (red: 2004; green: 2005; blue: 2006).

Discussion

The findings of this study are similar to those of other studies investigating coyote home ranges and survival in similar habitats. However, only recently has research on the behavior and ecology of the coyote population in Ohio been conducted, and this is the first detailed report of such data. Although coyotes have been the subject of numerous studies throughout the United States, their elusive nature greatly restricts the type of data collected. However, more knowledge about this successful medium-sized carnivore is sorely needed as its range expands and management practices are reconsidered.

Coyotes in Ohio are often believed to be "eastern coyotes." Whether a genetically distinct coyote variety exists in the northeastern region of North America has been debated in the literature over the past several years. Recently, Way (2007) analyzed reported body masses of coyotes throughout the United States to determine whether differences were correlated with the longitude of the region in which the animal was found. His results suggest that the body mass of coyotes is strongly correlated with the longitude of their location. He found male weights averaged 16.4 ± 1.5 kg (range: 14.2 – 20.4 kg) and female weights averaged 14.7 ± 1.6 kg (range: 11.9 – 17.9 kg) in the northeast (i.e., longitude < 80°). Based on the regression lines of his analyses, coyote body mass west of 80° longitude (i.e., 80° - 155°) averaged 12 kg for males and 9 kg for females. Although his study lacked data for the region from 80° - 84° longitude, in which Ohio is located, his regression line suggests that body mass should average 14 kg and 12.5 kg for males and females, respectively, in this region. The average weights of the coyotes in the study presented here are closer to those reported for coyotes in the northeast than to those in more western regions. Although the Ohio coyotes may be larger than their western counterparts, they still did not approach the sizes believed to be typical by many local residents (i.e., >23 kg). Even in the northeast, validated reports of coyotes >23 kg are rare (Hilton, 1978; Jonathan G. Way, personal communication, March 26, 2003).

In most studies of coyote behavioral ecology, animals are categorized to reflect their range, social, and/or reproductive status. Limited data in this study restricted our knowledge of the latter two status categories. Home range status (e.g., resident or transient) was determined through radio tracking of the collared animals. Range classification of coyotes in similar studies has been determined using several methods. In their study of coyote space and habitat use on a military reservation in Kansas, Kamler and Gipson (2000) based their classification of animals as residents or transients on a) the size of the animals range (“small” or “large,” respectively), and b) whether the animal was seen associating with other coyotes (resident) or traveling alone (transient). Grinder and Krausman (2001), in their study of urban coyote home ranges and habitat use in Arizona, considered a radio-collared coyote to be a resident if it used a unique area for ≥1 biological season and if the researchers were able to locate the animal in ≥70% of all attempts. Transients were defined as animals that could only be located in ≤50% of all radio-location attempts and that moved over a large area in a nomadic fashion. Gese et al. (1988) also classified coyotes as residents if they used one territory for ≥1 season or transients if they showed no permanent affinity for one area. Roy and Dorrance (1985) characterized coyote movement as “dispersal movements” if the animal traveled more than 5 km without returning for over 10 days.

The methods of classifying coyotes’ home range status used in the studies described above were not always feasible in the present study. I had limited data on the social or reproductive status of individual animals, which can be useful in determining whether an animal is a resident. The duration of individual radio-tracking sessions in this study were variable, with the researcher searching by vehicle for several hours or tracking by airplane when animals were not located in areas in which they had previously been found. In most cases, animals were eventually located; therefore, categorizing animals in this study using percentage of successful location attempts was not valid. The calculation of mean distances between consecutive locations – in a data set in which time between location estimates was standardized – accurately reflected changes in an individual’s ranging behavior. Changes in ranging distance over time may provide a better descriptor of a coyote’s resident status than changes in the researcher’s ability to locate individual animals. Data from future studies with larger sample sizes might reveal patterns in distance-between-location measures that could lead to an additional, reliable metric for classifying animals.

Resident coyotes in agricultural-suburban landscapes have been reported to traverse home range areas ranging from 2.9 – 74 km^2 (Atwood et al., 2004; Berg and Chesness, 1978; Person and Hirth, 1991). This wide variation in home range size has been attributed to a variety of factors, including the individual animal’s sex (Berg and Chesness, 1978; Laundré and Keller, 1984) and social and reproductive status (Gese et al., 1988; Mills and Knowlton, 1991; Pruss, 2002), prey availability (Atwood et al., 2004; Mills and Knowlton, 1991; Woodruff and Keller, 1982), habitat quality (e.g., availability of vegetation for protective cover and food, landscape fragmentation) (Atwood et al., 2004; Gese et al., 1988; Grinder & Krausman, 2001; Holzman et al., 1992), level of human activity and exploitation (Atwood et al., 2004; Grinder and Krausman, 2001; Mills and Knowlton, 1991; Woodruff and Keller, 1980), population density (Woodruff and Keller, 1982), and seasonal differences (Holzman et al., 1992; Mills and Knowlton, 1991). These factors are believed to affect home-range size individually and as inter-related phenomena.

The sample size for resident animals in this study was too small to statistically analyze differences between home range sizes. However, range sizes for four of the five small-range residents, plus the two animals who settled into small ranges, were similar in size. Two of these animals, M703 and F763, were residents in areas that were a blend of suburban development, including some commercial facilities, and agricultural fields. These animals were most often located in the agricultural expanses or wooded areas of commercial lands within their ranges, not within residential developments. Because coyotes are predators of primarily small mammals, it is not surprising that their range sizes would not differ greatly between agricultural and suburban-agricultural landscapes. Although animals that range in more developed areas need to maneuver through fragmented habitats, these suburban landscapes typically contain abundant small-mammal prey species (e.g., cotton-tail rabbits and various rodent species).

The diurnal and nocturnal core area estimates of the small-range resident coyotes illustrate a pattern of behavior described by other researchers. In areas where coyotes are persecuted, as they are in agricultural regions of Ohio, they tend to move most during crepuscular or night-time hours (Andelt, 1985). This could explain the significant differences found between diurnal and nocturnal ranges. In addition, coyotes tend to rest during the day in protected areas (e.g., woods or tall grass), away from human activity (Atwood et al., 2004; Grinder and Krausman, 2001; Person and Hirth, 1991). With the exception of M582's 2004 data, the diurnal core areas were located within the nocturnal cores, suggesting that these were areas in which the animals felt safest and returned to most often to rest. Atwood et al. (2004) reported that forested habitat was predominant in the 50% UD contours of his study animals in Indiana. In my study, all of the diurnal core (50% UD) areas contained wooded regions and were typically in a location remote from human activity. In fact the researcher would typically expect to find an animal in "his/her woodlot" when tracking the coyotes during day-time hours.

Further speculation on reasons for the variation among resident home-range sizes in my study would be impractical due to the lack of habitat-use data and the small sample size of resident animals available. It should also be noted that the estimator (e.g., kernel methods, minimum convex polygon, harmonic mean) used to calculate home range size affects the resulting measurement (Hernández and Laundré, 2003; Laundré and Keller, 1984; Shivik and Gese, 2000), so comparisons between studies should be reviewed cautiously. Even the same estimator has been found to produce quite different results between different software packages, depending upon the algorithm employed by the program (Mitchell, 2006).

As indicated by the mortality data presented here, coyotes in central Ohio are highly persecuted by hunters and trappers. The average time period that a coyote was radio-collared for this study was 8 months, with 13 out of 19 (68%) of the animals dying – most often due to human activity – during the study. Although this level of human-induced mortality seems high, it is substantially lower than percentages reported in studies conducted in western states (Windberg et al., 1985): 92% and 95% in Utah reported by Knudsen (1976) and Mills and Knowlton (1991), respectively; 93% in Wyoming (Tzilkowski, 1980); 83% in southern Idaho (Davison, 1980). Similar results to those reported here were found by Chamberlain and Leopold (2001) in their study of a radio-collared population of coyotes in Mississippi. In their study 50% of 16 mortalities were attributed to human activity (i.e., hunting) during deer and turkey hunting seasons. Other studies have reported the highest harvest of coyotes during winter fur-bearer trapping and deer-hunting seasons (Davison, 1980; Knudsen, 1976; Tzilkowski, 1980), and our results also followed this trend, with 9 of the 13 mortalities occurring from November through March, 8 of which were trapped and/or shot. Coyotes in Ohio are also legally shot during other months of the year, as there is no closed season on coyotes in the state. Numerous landowners told me that they and/or their neighbors attempted to shoot coyotes on sight when possible throughout the year.

Human activity has been reported to have substantial impact on the range expansion (Hill et al., 1987), home-range size, and mortality rate of coyotes in the United

States. The ever-increasing suburban sprawl nationwide will undoubtedly affect coyote populations. Long-term studies of resident animals in developing areas and their responses to such development are needed to better understand the effects this human activity has on coyote ecology and behavior, especially as the two species are brought into closer contact. Community educational programs are needed to provide local residents with accurate information about coyote behavior and ecosystem functioning to alleviate fears and allow people to change human behavior that might be encouraging coyotes to enter residential areas. Coyotes can thrive in any habitat that meets a threshold level of resources (e.g., food abundance and protective cover in which to rest and travel) (Grinder & Krausman, 2001). Further research, elucidating these ecological requirements of the coyote, would provide valuable information for residential planning and development that could greatly reduce human-coyote conflicts.

CHAPTER 3

CUES TO GROUP SIZE IN THE CHORUS HOWL OF THE COYOTE

Introduction

Conflict is costly in terms of energy use and the potential for injury or death. Therefore, it is selectively advantageous for an animal to assess its chances of winning a contest and withdraw from conflict if those chances are low (Enquist & Leimar, 1983; Hammerstein, 1981; Maynard Smith, 1982; Maynard Smith & Parker, 1976; Parker, 1974). Game-theoretical models of agonistic behavior suggest that animals should base decisions about conflict escalation on an assessment of their opponent's fighting ability or resource-holding potential (RHP).

Aggressive displays, including some vocalizations, are believed to function as advertisements of an animal's RHP that allow a competitor to assess its chance of winning in a direct conflict (Clutton-Brock & Albon, 1979; Parker, 1974). Studies of such advertisement displays have historically focused on contests between individuals. However, more recent studies have investigated whether correct assessment of group size is important in determining potential costs in contests between groups (Kitchen, 2004; McComb et al., 1994; Radford, 2003; Seddon & Tobias, 2003; Wilson et al., 2001).

These studies have measured the responses of group-living animals to group vocalizations of conspecifics, investigating whether the size of a potentially invading group affects the response of a territory-holding resident. The results of these studies suggest that long-distance vocalizations provide conspecifics with information about a competing group's size, allowing the receiver(s) to assess its odds of winning and decide whether or not to enter into direct conflict with the intruders.

The structure of the coyote group yip-howl (the name applied to coyote chorus howling by Lehner (1978a, 1978b)), as it is described in the literature, suggests that information about group size might be available in the signal. Lehner (1978b) explained that "a group yip-howl bout is generally initiated by one individual…, which is then joined by others. The initiator generally gives a long, relatively un-modulated howl. As more individuals join in, the howls become more amplitude and frequency modulated and yipping occurs, gradually becoming more frequent" (p. 718). This structural pattern can potentially reveal information about the number of howling participants. Two components in particular, timing of entry into the chorus and fundamental frequency (f_o) of an individual's howl, could allow receivers to "hear out" the number of individuals howling. Research into the ability of humans to hear out separate sound sources in a complex sound has shown these features of sound to play an important role (Moore, 1997).

The sequential entry of individual voices into the chorus could allow listeners to discriminate the number of individuals vocalizing. Asynchrony in sound onset is a cue used by humans to hear out the sources of complex sound (Moore, 1997), especially for sounds with fast attack times (i.e., sudden transfers of energy) (Bregman, 1990). Joslin (1967) used this feature of wolf chorus howls to estimate pack size by ear, and found the method superior to any other he had employed. In addition, Lehner (1978b) suggested that the initial howls in the chorus are relatively constant in frequency; therefore, these sounds should propagate reliably through the environment.

Fundamental frequency is the second key feature used by humans to hear out individual sound sources. It has been found that people can distinguish between complex tones (e.g., those created by identical musical instruments) when each is playing a sound of a different f_o (Moore, 1997). It seems that this can best be achieved if the sounds differ in frequency by at least 6%, just slightly above the pure tone difference limen (DL; or just-noticeable difference, JND) (Scheffers, 1983). Tooze et al. (1990) used discriminant function analysis (DFA) to successfully identify the howls of individual wolves. The correct categorization of howls in this analysis was to a great extent dependent on differences in the f_o of individual howls.

Separately, asynchrony of timing and differing f_os of individual voices can be effective cues for hearing out individual sound sources in human audition. In the context of the howling chorus, the presence of both cues would seem beneficial. As discussed previously, researchers in the field often try to count the number of canids (wolves or coyotes) entering a chorus to determine the size of the vocalizing group. However, once an individual animal’s howl ended and another howl began, the researcher – without seeing the animals – could not be sure whether the latter howl was produced by the first or a different individual. Unique voice characteristics would allow listeners to distinguish between individual animals, and thus know whether the same animal re-enters the chorus.

Individual voice characteristics (e.g., f_o) could also provide cues to group size by increasing the overall sound complexity of the chorus. Additional voices of the same f_o would possibly increase the intensity of the chorus, providing a cue to increased group size; however, voices of differing f_os would also increase the spectral complexity of the chorus. Along with varying onset/offset times of vocal signals and overlap among individual voices, more specific information about group size would be available (McComb et al., 1994; Radford, 2003).

The purpose of the study described here was to determine whether acoustic cues for group size are present in the chorus yip-howl of coyotes. Chorus howls of captive coyote groups were recorded, and the vocalizations of individual animals were identified using video recordings of the howling bouts to code sound spectrograms of the chorus. These spectrograms were then used to measure various acoustic parameters of individual howl vocalizations, including: frequency (f_0, minimum, maximum), duration, and spectral contour. The beginning time of each vocalization was also measured to determine time of entry into the chorus for each individual. Statistical analyses of these acoustic variables indicated that group size cues could be available to coyotes in the chorus howling of conspecifics.

In addition to analyses of acoustic measurements, a “substitute” (human) perceptual system was employed to better understand how coyotes might perceive conspecific howling choruses and “hear out” the number of vocalizing individuals.

Howling choruses produced by coyote groups of various sizes were played to human subjects, who were then asked to estimate the number of animals participating in the chorus. Results of this exercise indicated that humans can fairly accurately discern coyote group size from a howling chorus.

Methods

Subjects

Video and audio recordings of coyote chorus howls were collected at eight zoological facilities in the United States. Although 12 facilities were visited, coyotes at only eight of the sites vocalized during the hours of recording. Table 3.1 provides information about these recordings, including the facility names and locations, dates of visits, numbers of male and female coyotes in the group, and number of usable recordings collected. Facilities visited where no recordings were collected were: Clinch Park Zoo, Traverse City, MI; Wilderness Trails Zoo, Birch Run, MI; Space Farms Zoo, Sussex, NJ; Arizona-Sonora Desert Museum, Tucson, AZ.

Facility	**Location**	**Dates**	**Coyotes**		**Recordings**
			M	**F**	
Stone Zoo	Stoneham, MA	3/22/03 - 3/28/03	2	3	7
Queens Zoo	Flushing, NY	3/29/03 - 4/4/03	2	3	8
Garlyn Zoo	Naubinway, MI	9/19/04 – 9/20/04	2	1	3
Howell Nature Center	Howell, MI	9/24/04 – 9/25/04	2	0	5
Bear Mountain Zoo	Bear Mountain, NY	9/29/04 – 9/30/04	1	1	4
Living Desert Zoo & Gardens	Palm Desert, CA	10/31/05 – 11/2/05	3	0	9
Moonridge Animal Park	Big Bear Lake, CA	11/3/05 – 11/5/05	1	1	4

Table 3.1. Index of recordings collected at captive facilities.

Coyote groups were housed and on display together at all facilities, except Queens Zoo and Howell Nature Center. At Queens Zoo the entire group of five coyotes was never on display together due to aggression between one of the females and three of the other animals (the other two females and one of the males). To accommodate these behavioral issues, the two males and the two other females were placed on display four days per week, and the aggressive female and the one male with whom she could interact were on display three days per week. This, of course, meant that one male was part of both exhibit groups. Five of the eight recordings were collected while the group of four was on display, and the remaining three recordings were collected while the two animals were on display.

The two male coyotes at the Howell Nature Center were housed in adjacent enclosures, separated by chain-link fencing. Although physically separated, the two males behaved affably toward one another at the fence line, chorus howled together, and would move nearer to the fence during howling bouts, suggesting they considered themselves part of a single social group.

The chorus howling bouts typically included all animals in the captive group. However, in three of the groups one individual never joined in the chorus howls: one female at Queens Zoo (in the group of four); one male at Garlyn Zoo; and one male at Living Desert Zoo & Gardens. These animals were often the targets of aggression from other members of their captive group; therefore, it is possible that their position within the social group prohibited them from participating. Or, it may be that these animals were not considered to be part of the social group but were forced by captivity to remain in close proximity to group members.

Recording Howling Bouts

The coyote groups at Stone Zoo and Queens Zoo were videotaped using two Panasonic AG-188 VHS camcorders and a Panasonic PV-DC352 digital video camcorder. All other groups were videotaped using a Sony CCD-TR940 Handycam 8mm video camera and the Panasonic PV-DC352 digital video camcorder. Audio recordings were collected using a Sony TC-D5 Pro II cassette recorder with an AT815a microphone contained within a wind zeppelin and muff.

Video and audio recordings were collected at each facility during the normal hours of operation, typically between 08:00 and 18:00, as well as immediately before opening and/or after closing when possible. Both spontaneous and elicited howling choruses were recorded (Table 3.2). Spontaneous choruses were defined as bouts commenced by the group without any prompting stimulus provided by the researcher. Elicited bouts were those produced in response to a prompting stimulus: either a person or persons howling near or in the enclosure, or the playback of a recording of an unfamiliar coyote chorus howl or a recording of an emergency siren played from a portable Audiovox DM8220S CD player through an Audix PH-3s or Nagra DSM speaker located in a position out of the coyotes’ view and at a distance of at least several meters from the enclosure. Choruses were considered to be spontaneous, however, if they followed a naturally-occurring stimulus, such as a real emergency vehicle siren within audible distance or a spontaneous howling chorus of captive wolves at the facility.

Attempts to elicit howls were made when the captive group did not spontaneously produce a chorus howl within an hour or two after equipment was set up and then at intervals of 90 to 150 minutes thereafter if spontaneous bouts were not produced.

Facility	**No. of Coyotes Howling**		**Recordings**	
	M	F	**Spontaneous**	**Elicited**
Stone Zoo	2	3	7	0
Queens Zoo	2	2	8	0
Garlyn Zoo	1	1	1	2
Howell Nature Center	2	0	0	5
Bear Mountain Zoo	1	1	1	3
Living Desert Zoo & Gardens	2	0	2	7
Moonridge Animal Park	1	1	2	2

Table 3.2. Index of spontaneous and elicited howling bouts recorded at captive facilities.

With the exception of Garlyn Zoo and Howell Nature Center, where two people filmed with handheld video cameras, video recordings were collected using one handheld video camera and one or two stationary cameras mounted on tripods outside the enclosure. All recording was conducted from outside the animals' exhibit enclosures, within several meters of the enclosure barrier. Depending upon the size of the enclosure, equipment was at a distance of approximately 2 to 100 meters from the vocalizing animals. At the 8 facilities from which howling choruses were recorded, the presence of the equipment and operator(s) did not appear to affect the behavior of the animals, aside from general curiosity during setup. As captive animals, regularly on display for the public, the groups were accustomed to people performing various tasks and watching them from within the areas in which the recording was done.

Digitizing Recordings

One recording of each howling bout collected at the captive facilities was selected to be digitized and analyzed. A recording containing the complete howling bout with the least extraneous noise was chosen from the various video and audio recordings collected. Recordings were digitized at 50 kHz with 16-bit amplitude resolution and saved as individual files using RTSD, an analog-to-digital conversion program (Engineering Design, 1999), and a low-pass anti-aliasing filter. The digitized recordings are archived in the collection of the Borror Laboratory of Bioacoustics at The Ohio State University (http://blb.biosci.ohio-state.edu).

Coding Spectrograms

Randomly selected video recordings of each captive group were reviewed by three people (the author and two assistants) to determine the types of vocalizations produced by the coyotes during the howling choruses. A consensus was reached to identify the following vocalizations using agreed-upon features distinguishable by ear: howls, screams, barks, woofs, yips, growls, whines, yelps, and a vocal type we referred to as 'yi-ing.' Although some descriptions of vocalizations referred to by these names are provided in the primary literature for both wolves and coyotes, these descriptions did not necessarily serve as the classification scheme upon which the vocalizations in this study were categorized. Therefore, descriptions of these vocalizations as they apply to this research are provided in Table 3.3.

Vocalization:	**Description:**
Howl	A long (≥0.4 sec) vocalization of relatively stable frequency, most often perceived as an ‘oo’ sound.
Scream	A long (≥0.4 sec) vocalization, generally higher in pitch than a howl and often decreasing in frequency over time.
Bark	A short burst (<0.4 sec) of often noisy broadband sound, most often perceived as a ‘ruff’ sound.
Woof	A short burst (<0.4 sec) of broadband sound, of lower amplitude than a bark and perceived as a ‘woof’ sound.
Yip	A short burst of sound of higher f_0 than a bark or woof and often harmonic in structure.
Growl	A low-frequency (<1 kHz), broadband sound of moderate duration.
Yelp	A short burst of high-frequency (>1 kHz) sound often harmonic in structure.
Whine	Similar to a yelp in frequency and structure, but of longer duration.
Yi-ing	A continuous amplitude-modulated vocalization, typically long in duration and often produced by opening and partially closing the mouth resulting in a ‘yi-yi-yi’ sound.

Table 3.3. Study-specific definitions of coyote vocalizations. (Note: For analyses howls and screams were both treated as “howls” and barks and woofs were treated as “barks.”)

Audio spectrograms (2048-point FFT, time resolution = 40.96 ms) with normalized amplitude grayscale and time and frequency axes were produced using the digital sound analysis program SIGNAL (Engineering Design, 1999) and an HP Laserjet 6P printer. The printed spectrograms were then coded to indicate which individual animal in a group produced each vocalization based on video footage of the howling bouts. Short segments of video played back on a television monitor were viewed while the corresponding spectrogram segment was viewed and played back in RTSD, allowing observers to identify which individual animal was associated with each vocalization on the printed spectrogram. Not all vocalizations could be assigned to an individual, either because the animal or its exact behavior could not be identified in the video or because the vocalizations of several animals overlapped in an indistinguishable manner in the spectrogram and could not be isolated.

Acoustic Analyses

Acoustic features of the howling bouts were measured using SIGNAL. A customized program written within SIGNAL was used to measure specific features. Howls and barks were the primary vocalizations of interest, and were also the most easily extracted from the howling bouts and assigned to individual animals. Ten variables were measured for each howl and bark vocalization. Call duration, beginning frequency, end frequency, minimum frequency, maximum frequency, time of minimum frequency within the call, and time of maximum frequency within the call were measured using a cross-hair cursor on a spectrogram generated using a 2048-point Fast Fourier Transform (FFT) with an upper frequency limit set at 4000 Hz (Figure 3.1). At the point of maximum frequency, the peak (or dominant) frequency, the fundamental frequency, and the relative amplitudes (re: peak amplitude) and frequencies of up to 10 harmonics present were measured from a power spectrum based on an 8192-point FFT with an upper frequency limit set at 8000 Hz (Figure 3.2). In addition to these features, the vocalization’s serial position within the bout was also recorded.

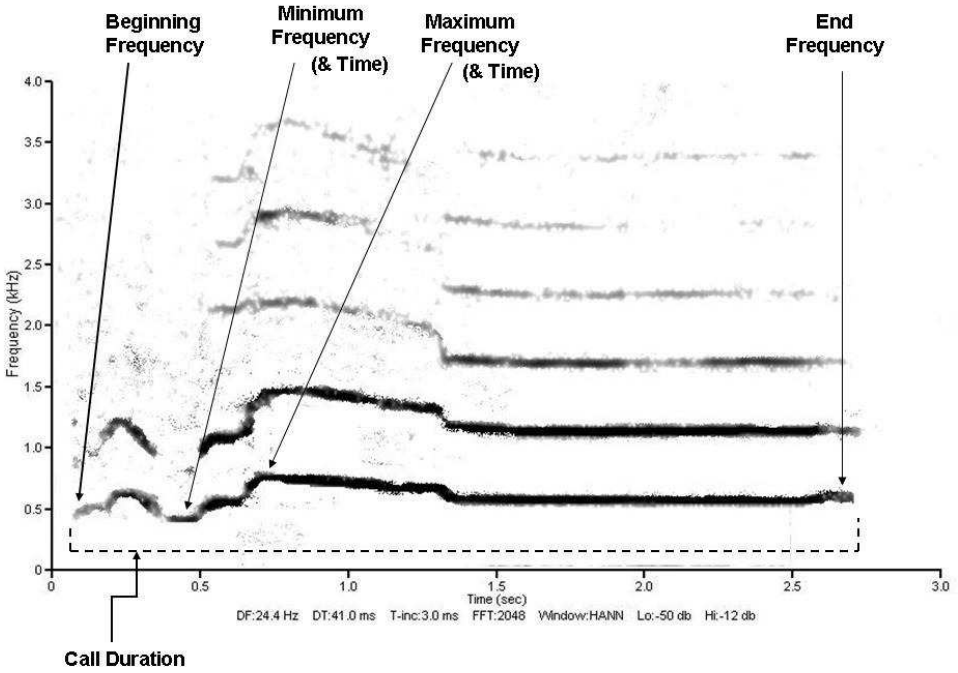


Figure 3.1. Annotated spectrogram indicating measurements taken on vocalizations.

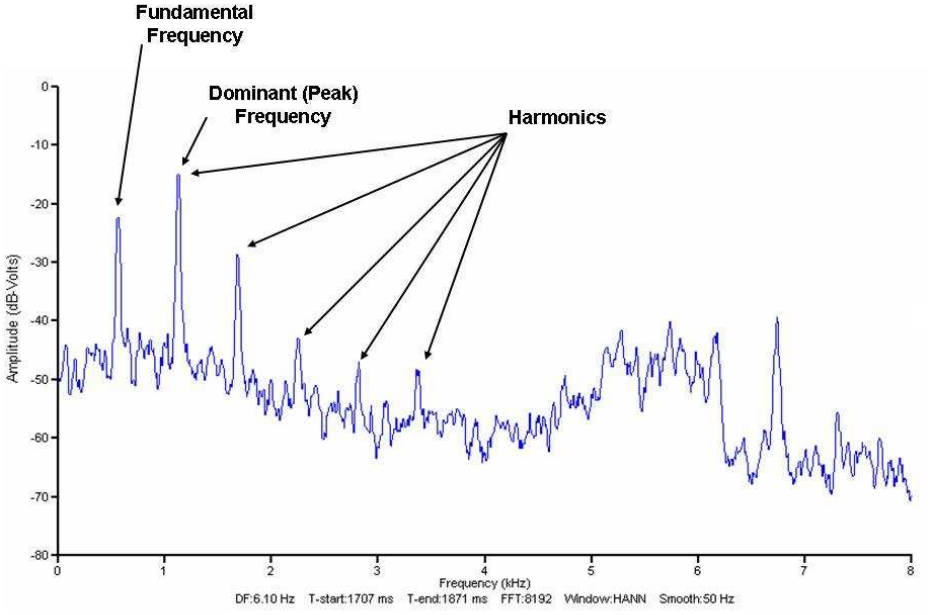


Figure 3.2. Annotated power spectrum indicating measurements taken at point of maximum frequency within vocalization.

Howls and barks differ from one another acoustically. In addition, there is a great deal of variability within each of these vocal types. To better describe and analyze this within-category variability, certain howl-specific and bark-specific analyses were performed in addition to the common measurements described above.

Howl Measurements

Howls are often described as flat-frequency (or constant frequency) vocalizations when compared with other coyote vocalizations (Lehner, 1978a; McCarley, 1975). As shown in the sample howl contours displayed in Figure 3.3, most howl types do contain portions of relatively stable frequency, fluctuating little over the entire duration of the call. However, it is also evident from this figure that the frequency of these relatively long vocalizations can vary temporally across the signal, rising, falling, or warbling up and down. Yet howls stand out perceptually (to humans) as distinct vocalizations. This is most likely due to the howl's production during a single exhalation cycle, providing it with perceptual continuity. The scream vocalization shares this characteristic and is similar in length and structure to calls categorized as howls. For these reasons scream vocalizations were treated as "howls" in the acoustic and statistical analyses.

Because howls, and the flat portions of howls in particular, were hypothesized to be most likely to contain information about group size, I sought to comprehensively describe the acoustic structure of these vocalizations. To accomplish this, a program was written within SIGNAL to perform additional measurements on the flat portions of howl vocalizations. A flat portion was defined as a segment greater than or equal to 0.4 s in duration that did not vary over its length by greater than 100 Hz. Variables measured for flat portions included: duration; frequency at the beginning; frequency at the end; and frequency of “mid”-point and the time of this measurement within the flat segment. Note that “mid”-point is a loosely descriptive term in that it refers to a point within the flat portion at which there was the least amount of noise interfering with the target signal. At the “mid”-point, the peak (or dominant) frequency, the fundamental frequency, and the amplitudes and frequencies of up to 10 harmonics present were measured from a power spectrum based on an 8192-point FFT with an upper frequency limit set at 8000 Hz. Amplitude values were normalized relative to the highest amplitude peak, which was set to 0 dB. In addition to these variables, a binary value of 0 or 1 was recorded to indicate the absence or presence, respectively, of a “missing fundamental.” A vocalization was considered to have a missing fundamental if the overtones of the signal formed a harmonic series and suggested a f_0 that was completely absent from or at an undetectably low amplitude within the sound spectrogram. In human audition the pitch of the f_0 is the perceived pitch of a sound even when the f_0 is missing (Bregman, 1990). In cases of a missing fundamental in the data set, the f_0 was calculated from the harmonic peak intervals and manually entered into the output file to be used in the subsequent statistical analyses.

Another acoustic parameter of potential importance in fully describing the howl vocalizations was the spectral contour of the sound. The spectral contour reflects the changes in frequency, or the frequency trajectory, over the temporal duration of the signal. To best depict the frequency changes (i.e., acoustic shape) of the howls, SIGNAL’s DRAW function was used to produce frequency contours of all measured howl vocalizations at the point of greatest intensity within the frequency band by tracing the frequency contour of the sound directly on the spectrogram image using a cross-hair cursor. The spectrograms used for contour drawing were generated using a 2048-point Fast Fourier Transform (FFT) with an upper frequency limit set at 4000 Hz.

To categorize the contour shapes, printed versions of 323 drawn frequency contours, representing all measured howls, were independently sorted by three judges (the author and two other members of the Borror Laboratory of Bioacoustics). The judges were asked to sort the contours based on the 17 categories shown in Figure 3.3. These categories were created by the author based on a preliminary review of the printed contours.

After the printed contours were sorted, the original 17 categories were grouped into six broader classifications: FLAT, INCREASING, DECREASING, FLAT WITH CHANGE, CHANGING, and WARBLY. The FLAT category incorporated the original Flat howl type only. INCREASING incorporated the Rising and Step-Up types. DECREASING incorporated the Falling and Step-Down types. FLAT WITH CHANGE incorporated all types that had a flat component mixed with a segment that changed in frequency. CHANGING incorporated the U-Shaped, Arched, and Irregular types. WARBLY incorporated only the Warble howl type. These six categories were assigned numeric labels and added to the data set of howl measurements.

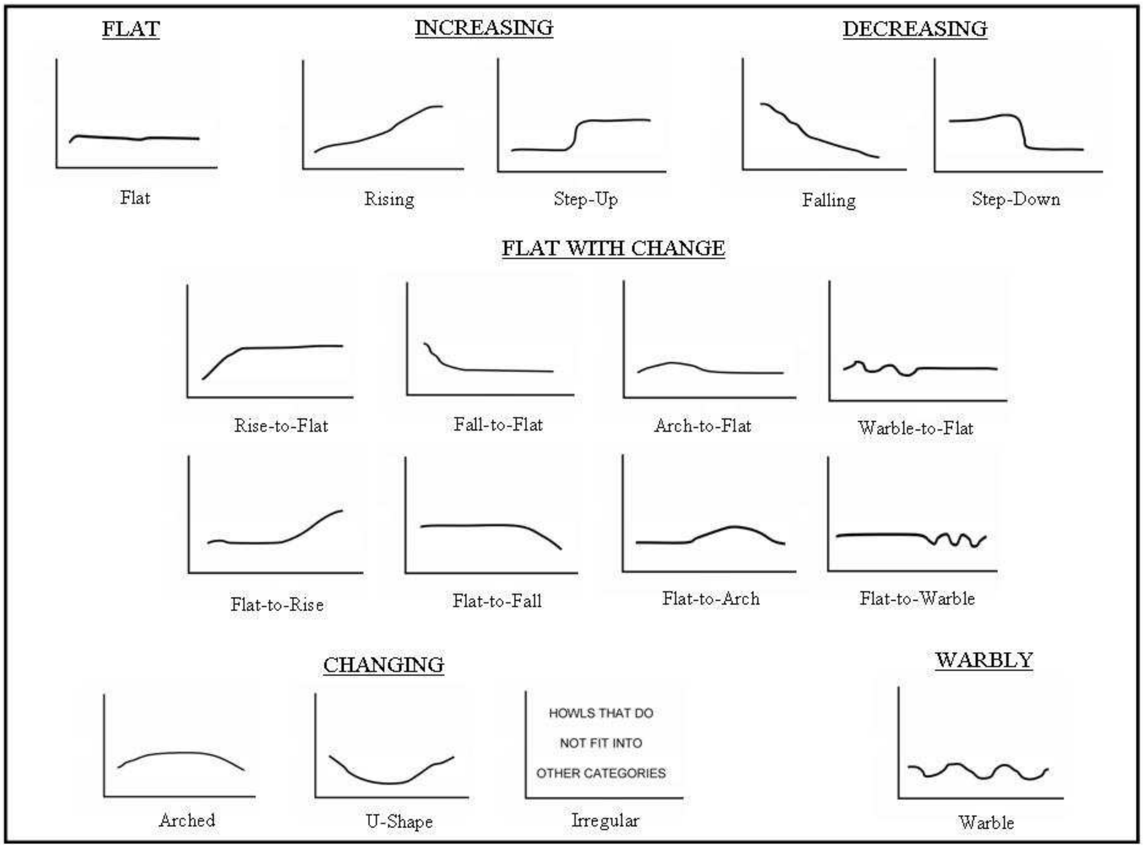


Figure 3.3. Representations of sample howl contours used as guide for categorization in visual sorting task. (X axis represents time; Y axis is frequency.)

Bark Measurements

Barks were short, variable vocal bursts that sounded “harmonic” or “noisy” to human listeners. The frequency contours of barks were less complex than those of howl vocalizations; therefore, the “shapes” of barks in these analyses were derived from the frequency measurements at the beginning and end of the bark, plus the minimum and maximum frequencies within the signal and the times associated with them. These frequency measurements provided the necessary information to infer shape since bark contours typically fall into one of the following categories: flat, rising, falling, or peaked.

These acoustic parameters have been used to describe bark vocalizations in both coyotes and domestic dogs (Riede et al., 2005). The methods used in the present study for frequency contour classification and harmonic-to-noise ratio determination were based on those in Mitchell et al. (2006) and Riede et al. (2005), respectively.

Coyote barks range in acoustic structure from “clear” and harmonic to “noisy” and broadband. These differences probably result from variations in the structure of the animal’s vocal tract and reactions of structures within the tract (e.g., the vocal folds and upper vocal tract) when air is exhaled during production of a sound. To determine the “noisiness” of the barks, a harmonic-to-noise ratio (HNR) was calculated. The HNR estimated the maximum difference between the “harmonic spectrum” and the “noise spectrum” of a bark. A programming routine (provided by Brian Mitchell) within the customized SIGNAL program used to measure the coyote vocalizations automated the calculation of the HNR. A 50-ms segment, centered around the maximum frequency of the bark, was chosen for this analysis. This segment was then divided into seven 20-ms regions, with each region overlapping 75% of the successive region. The “harmonic spectrum” was produced by averaging individual 512-point FFTs calculated for each of the seven regions. The “noise spectrum” resulted from smoothing the harmonic spectrum using a 10-point (488 Hz) moving average. The noise spectrum was then subtracted from the harmonic spectrum after removing all energy present below 500 Hz and above 4 kHz to determine the HNR (Figure 3.4).

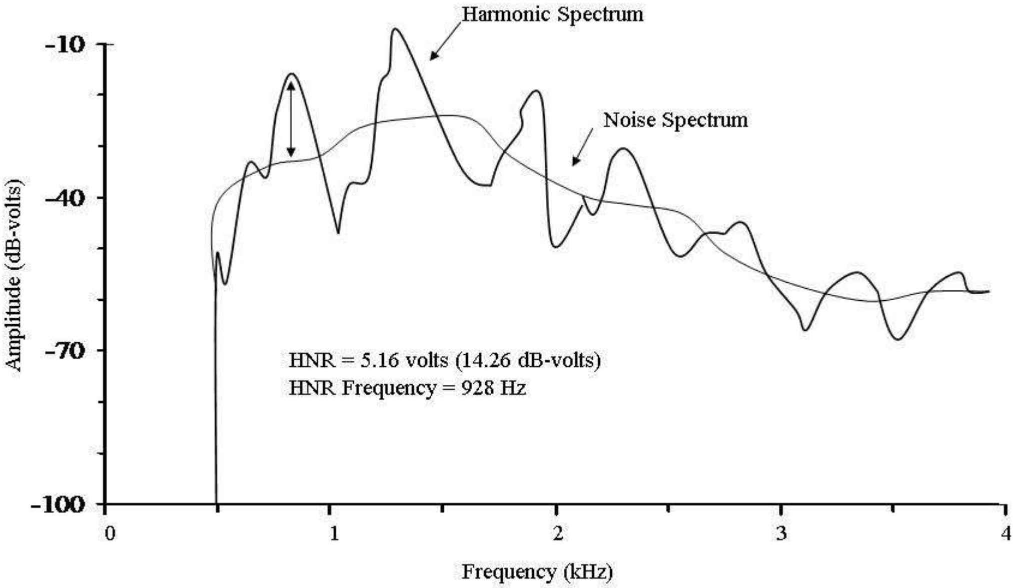


Figure 3.4. Example of the Harmonic-to-Noise Ratio (HNR) calculation (adapted from Mitchell, 2004)

Statistical Analyses

Differences in vocal characteristics between individual coyotes within a social group were of primary interest in this study. The ability to discriminate between the voice characteristics of individuals could be of significant importance to conspecific receivers in determining the number of animals participating in a howling chorus.

Howl Data Analyses

To understand the dominant factors underlying the variable set and reduce the number of variables to be used in subsequent analyses, a principal components analysis (PCA) was performed on the complete data set of howls from all zoo groups, except the NWT group, using 19 variables from the original SIGNAL program data output and four variables from the SIGNAL program measuring the flat components of the howls (Table

3.4). These variables were log transformed to produce more nearly normal distributions prior to running the PCA. With missing values replaced with the mean and eigenvalues of ≥1.0, the PCA resulted in six principal components, as shown in Table 3.5. These six components were used as the independent variables in discriminant function analyses (DFAs) performed separately for each group of zoo coyotes. Four of the social groups (BMZ, GZ, HNC, and MR) consisted of two individuals. One of the groups (LD) consisted of three individuals, but only two participated in howling choruses. Two groups (SZ and QZ) consisted of five individuals but only three individuals in each vocalized enough (N > 7 howls total) to be included.

Bark Data Analyses

Similar analyses were performed on the bark acoustic measurements as were performed on the howl data. A PCA was run on the complete data set of barks from all zoo groups. Again, variables were log-transformed prior to this analysis, and a total of 18 variables were entered into the PCA (Table 3.10). With missing values replaced with the mean and eigenvalues of ≥0.95, the PCA resulted in five principal components, as shown in Table 3.11. These five components were used as the independent variables in discriminant function analyses (DFAs) performed separately for each group of zoo coyotes for which bark data was available. Prior probabilities in these DF analyses were calculated using observed group sizes.

Human Estimates of Group Size

Twenty-one human subjects participated in this exercise. Each subject heard six segments of recorded coyote yip-howl chorusing, taken from recordings collected at the zoo facilities, described above. Three of the segments consisted of the INTRO portion of a chorus and three segments contained a portion of the YIP section. The INTRO segments were created by cutting out the first several seconds from a complete chorus. The length of the segment extended to the point by which each individual in the chorus had howled at least once. Segments ranged from 5.4 s to 15.2 s in length. The YIP segments were taken from later points in the chorus when most animals were yipping, barking, and yi-ing. There was no overlap between INTRO and YIP segments extracted from the same chorus recording. YIP segment lengths were matched to the lengths of INTRO segments.

A total of 33 INTRO and 33 YIP segments were created. There were 17 segments of each type for groups of two coyotes and nine segments of each type for groups of three coyotes. There were four INTRO segments and three YIP segments from groups of four animals; and three INTRO segments and four YIP segments from groups of five. The number of segments of each type within each group size was dependent on the number and quality of complete chorus recordings and whether segments meeting the above criteria could be extracted from them. All six segments presented to an individual subject were matched for length, and the order was randomized for group size and INTRO/YIP presentation.

All recordings of a group size of three were collected from the Queens Zoo coyote group. All recordings of group sizes of four and five were collected from the Stone Zoo group. Due to the limited number of captive coyote groups in the United States from which to collect recordings, this pseudoreplication was unavoidable. However, the researcher varied the six-segment composition to present the most diverse arrangements possible, although flexibility was limited by the segment-length matching criterion.

The human subject pool consisted of undergraduates, graduate students, and staff at The Ohio State University. Participants voluntarily agreed to participate in response to a mass email request for volunteers distributed by the researcher to undergraduate classes and research facilities at the University. The exercise was run with subjects individually at the Borror Laboratory of Bioacoustics. The researcher described the exercise to each participant, also providing a sheet of written instructions containing the same content. Participants were told that they would be listening to six audio segments taken from recordings of coyote yip-howl choruses, but no information about the size range of the groups or their captive (vs. wild) status was provided to the subjects.

Each participant was given a set of data sheets that called for them to estimate the number of coyotes they heard in each segment and describe the cues they used to determine each estimate. Again, the participants did not receive any instructions, either written or verbal, describing the types of cues to which they should be listening. Since most of the participants were unfamiliar with coyote vocalizations, the researcher played two sample yip-howl chorus recordings prior to the start of the exercise. Neither of these samples was a chorus from which test segments had been extracted.

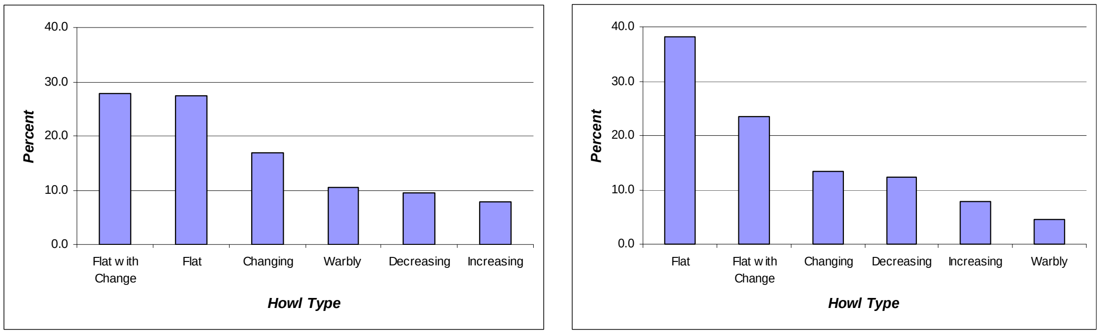
Participants listened to the segments through headphones on a personal computer using Microsoft Media Player. The recordings were identified only by the numbers 1 – 6. Participants were asked to listen to the segments in numeric order, listening to each segment twice and completing the data set information for that segment before moving on to the next. The researcher met with each participant at the conclusion of the exercise and reviewed their data sheet comments with them to ensure that the researcher understood the information provided.

Results

Spectral Contour Categorization

There was a high level of agreement among the judges sorting the spectral contours of howl vocalizations. Eighty-seven percent (281) of the contours were sorted into the same category by at least two of the three judges, with 123 of those (38% of the total) being sorted into the same category by all three. None of the judges was in agreement on the remaining 13% (42 of the contours). The researcher reviewed these 42 contours and placed each into a category that seemed to best describe the vocalization based upon the individual contour and the judges' original classifications.

The most common howl types were those containing flat portions (i.e., in the categories of FLAT or FLAT WITH CHANGE). More than 50% of all howl types were of these types, both for the entire howl data set (55.3%) and for a subset of only the first howl produced by each individual within a chorus (61.8%) (Figure 3.5).



(a) (b)

Figure 3.5. Percentage of howl types observed in recordings of captive coyotes. Figure (a) represents howl types for the complete data set; (b) represents the first howl types produced by individuals within a howling chorus.

Howl Variation Between Individuals

The PCA, performed on the 23 acoustic variables, resulted in six principal components (PCs) with eigenvalues ≥1.0 (Tables 3.4 and 3.5). These six PCs accounted for 83% of the variance in the data set of 277 howl vocalizations from a total of 19 coyotes. Figure 3.6 shows the number of howls contributed per animal.

The six PCs were labeled based on factor loadings in the component matrix. PC1 was labeled "F_0" (fundamental frequency). The highest loading components in this PC were related to the f_0, with the single highest loading component being the f_0 of the flat portion of the howl. The second and third highest loading components were also related to the flat portion of the howl (the ending and beginning frequencies, respectively). The next three highest component loadings were the peak 2, peak 3, and peak 1 frequencies, respectively. These first three peaks are closely related to the f_0 in that they represent the first three harmonics (or the first three multiples of the f_0) in the frequency structure. The next 14 variables loaded in the PC are all related to frequency measurements, and the lowest loading four variables are related to the duration of the signal (call duration, logCDur; duration of flat portion, logFlDur) and the "shape" of the howl as suggested by the time of the maximum and minimum frequencies within the signal (MAX_T; MIN_T).

PC2 was labeled "Harmonics," since the five highest loading variables were those related to the upper peaks (peaks 6 through 10) of the howl's harmonic structure. The correlation coefficients for the remaining 19 variables were < 0.4.

PC3 was labeled "Duration," with the two highest loading variables being the duration of the howl and the duration of the flat portion of the howl. Again correlation coefficients were substantially lower for the remaining variables in PC3.

PCs 4, 5, and 6 were the most difficult to interpret. PC4 was labeled "Beginning Frequency," based on the highest loading variable for that component, the beginning frequency of the howl. PC5 was labeled "Shape," based on the two highest loading variables MAX_T and MIN_T, with correlation coefficients of 0.576 and -0.458, respectively. The correlation coefficients for the remaining 21 variables of PC5 were all < 0.4. PC6 was labeled "Dominant Frequency." As described earlier, the fundamental frequency of a vocalization is not always the dominant frequency. In some cases, the fundamental frequency is filtered out of the sound (a.k.a., the missing fundamental), resulting in a sound that is still perceived at the pitch of the fundamental, but whose dominant frequency is one of the sound's harmonics. The highest loading variable of this component was the dominant frequency of the howl.

Total Variance Explained

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings		
	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	10.128	44.033	44.033	10.128	44.033	44.033
2	3.088	13.426	57.459	3.088	13.426	57.459
3	1.998	8.686	66.145	1.998	8.686	66.145
4	1.625	7.065	73.210	1.625	7.065	73.210
5	1.220	5.305	78.515	1.220	5.305	78.515
6	1.037	4.508	83.023	1.037	4.508	83.023

Table 3.4. Total variance explained from PCA performed on howl data set, indicating six principal components extracted based on eigenvalues ≥1.0.

Component Matrix

	Component					
	1	2	3	4	5	6
log_fund	.782	-.348	.111	.407	.110	-.108
log_begf	.753	-.281	.083	.498	-.129	.021
log_endf	.767	-.384	.064	.230	.233	-.151
log_maxf	.786	-.346	.095	.410	.099	-.107
log_minf	.810	-.327	.063	.314	-.026	-.021
logffund	.870	-.120	.124	-.261	.099	.183
logDFreq	.236	-.242	.021	-.218	.046	.614
logCDur	-.164	.388	.801	-.011	.107	-.007
logFlDur	-.113	.299	.756	.180	-.016	.025
logFlBgF	.866	-.108	.129	-.217	.048	.206
logFlEdF	.866	-.137	.127	-.262	.125	.167
logP1Frq	.828	-.127	.058	-.301	.099	.056
logP2Frq	.853	-.028	.005	-.319	-.023	-.039
logP3Frq	.840	.079	.106	-.284	-.145	-.087
logP4Frq	.802	.174	.061	-.245	-.230	-.155
logP5Frq	.741	.348	-.056	-.127	-.291	-.255
logP6Frq	.684	.448	-.157	-.026	-.297	-.200
logP7Frq	.626	.573	-.190	.078	-.109	-.093
logP8Frq	.509	.660	-.233	.189	.092	.065
logP9Frq	.402	.690	-.199	.229	.350	.187
logP10Fr	.337	.665	-.151	.214	.378	.234
MIN_T	-.098	.310	.589	.208	-.458	.254
MAX_T	-.147	.129	.392	-.308	.576	-.448

Table 3.5. Component Matrix from howl data PCA analysis. Values in columns headed Components 1 through 6 represent the correlation coefficients between the original variables (shown in the first column of the table) and the newly derived components.

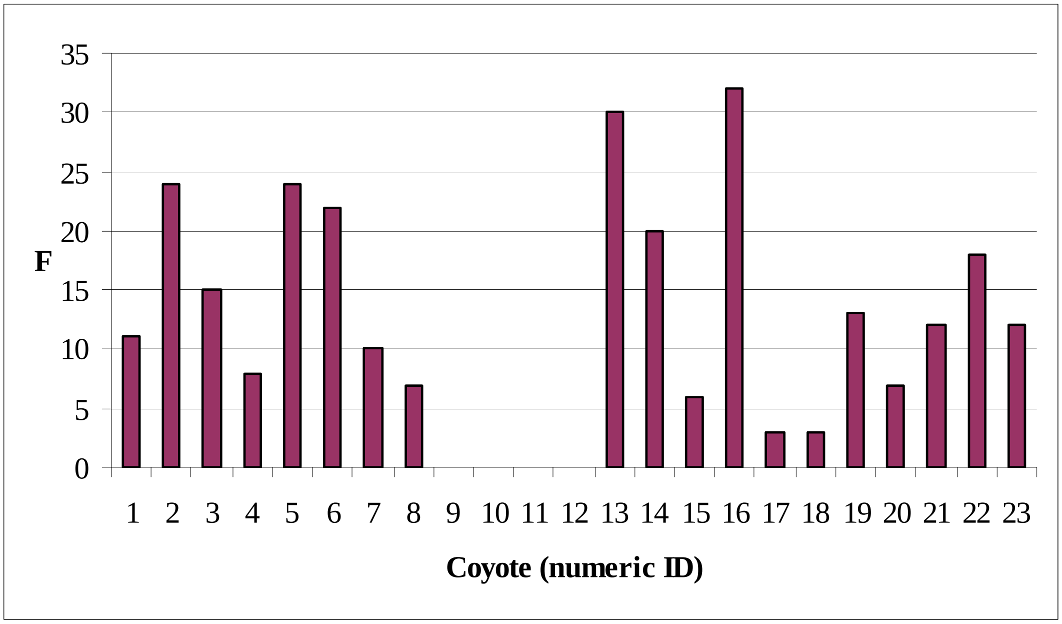
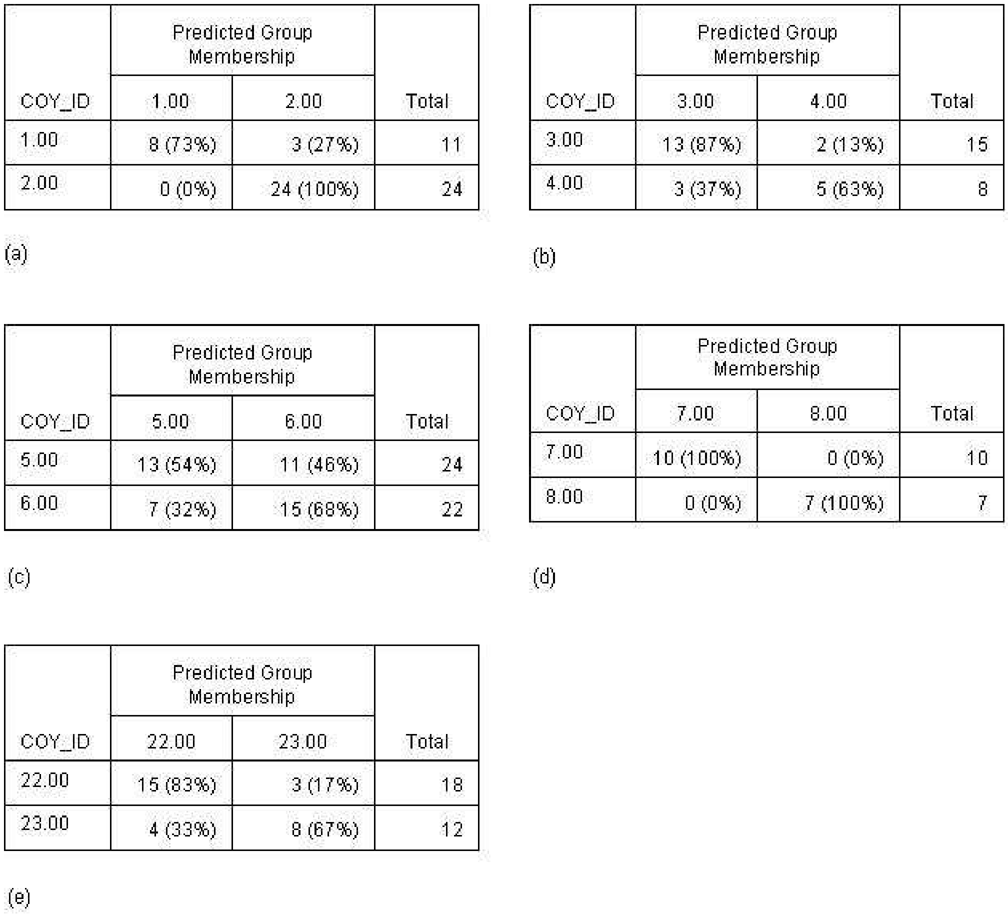


Figure 3.6. Number of howls per coyote contributing to the PCA. No howls from coyotes 9, 10, 11, and 12 (the NWT group) were included in the PCA.

The DFA analyses on the zoo groups' howl vocalizations resulted in an average of 82.9% correct classification of individuals overall, with cross-validated DFAs resulting in an average correct classification of 73.0%. In total, 265 howls were classified from 16 coyotes, representing seven social groups. The classification tables in Figure 3.7 display the results of the cross-validated DFAs for each of the groups of two coyotes. The tables in Figure 3.8 display the results of the cross-validated DFAs for each of the groups in which the howls of three individuals were analyzed.



COY_ID	Predicted Group Membership 1.00	Predicted Group Membership 2.00	Total
1.00	8 (73%)	3 (27%)	11
2.00	0 (0%)	24 (100%)	24

(a)

COY_ID	Predicted Group Membership 3.00	Predicted Group Membership 4.00	Total
3.00	13 (87%)	2 (13%)	15
4.00	3 (37%)	5 (63%)	8

(b)

COY_ID	Predicted Group Membership 5.00	Predicted Group Membership 6.00	Total
5.00	13 (54%)	11 (46%)	24
6.00	7 (32%)	15 (68%)	22

(c)

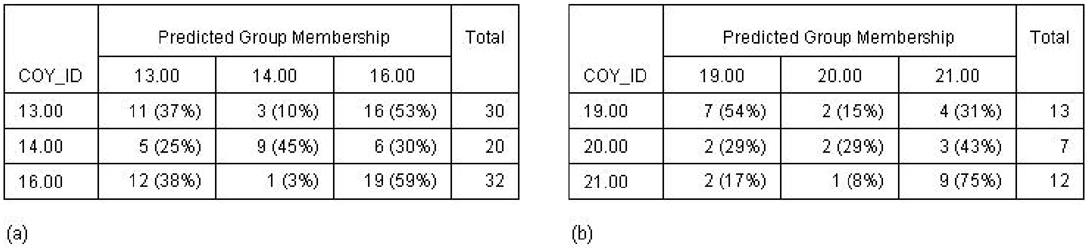
COY_ID	Predicted Group Membership 7.00	Predicted Group Membership 8.00	Total
7.00	10 (100%)	0 (0%)	10
8.00	0 (0%)	7 (100%)	7

(d)

COY_ID	Predicted Group Membership 22.00	Predicted Group Membership 23.00	Total
22.00	15 (83%)	3 (17%)	18
23.00	4 (33%)	8 (67%)	12

(e)

Figure 3.7. Classification results of cross-validated DFAs based on acoustic features of howls for coyotes within captive social groups of two animals. Tables represent captive groups: (a) BMZ; (b) GZ; (c) LD; (d) MR; (e) HNC.



COY_ID	Predicted Group Membership 13.00	Predicted Group Membership 14.00	Predicted Group Membership 16.00	Total
13.00	11 (37%)	3 (10%)	16 (53%)	30
14.00	5 (25%)	9 (45%)	6 (30%)	20
16.00	12 (38%)	1 (3%)	19 (59%)	32

(a)

COY_ID	Predicted Group Membership 19.00	Predicted Group Membership 20.00	Predicted Group Membership 21.00	Total
19.00	7 (54%)	2 (15%)	4 (31%)	13
20.00	2 (29%)	2 (29%)	3 (43%)	7
21.00	2 (17%)	1 (8%)	9 (75%)	12

(b)

Figure 3.8. Classification results of cross-validated DFAs based on acoustic features of howls for coyotes within captive social groups of ≥ 3 animals. Tables represent captive groups: (a) QZ and (b) SZ.

Wilks' lambda tests of significance revealed that the overall discriminant functions were significant for each group, except LD. Function 2 was non-significant for the two groups of three animals (QZ and SZ). The prior (expected) probabilities versus the actual cross-validated classification proportions for each animal are shown in Table 3.6.

Interestingly, the matrices of standardized canonical discriminant function coefficients for the groups' DFAs revealed that different discriminant loadings were more highly correlated with some groups than with others, often suggesting very different acoustic features were used within each group to discriminate between the howls of individuals (Table 3.7). The PC associated with f_0 (PC1) was highly correlated with the discriminant functions of three of the four groups with significantly discriminating functions (BMZ, MR, and HNC). However, PC6 (associated with dominant frequency) was the most highly correlated PC with the MR group's discriminant function (DF). Cross-tabulation of the individual animals in these five groups by the variable "missing fundamental" found that half of the howls produced by coyote F-7 (group MR) had a missing fundamental, whereas none of the animals in the BMZ or HNC groups had this vocal quality. Half of the howls produced by one of the two animals in the GZ group (F-3) also had the f_0 filtered from the signal. The most highly correlated discriminant loading for the GZ group, however, was call duration. The correlation coefficients of the discriminant loadings for the two groups of three coyotes (QZ and SZ) also differed. The most highly correlated PC on both functions 1 and 2 for the QZ group was PC2, which was related to the harmonic structure of the howls.

The misclassification of animals and the mix of discriminant loadings contributing most to the DFs in the SZ group were surprising. Especially surprising was the non-significant classification of coyote F-20. This particular coyote had a characteristically unique voice that was easily discernable by ear when listening to the SZ group's howling choruses. While measuring the individual howls, it was evident that F-20's howls, especially those emitted early in the chorus, were recognizably similar to one another and typically had a "missing fundamental." Based on these observations, a separate DFA was run on the SZ group using eight selected variables that might best represent the perceived sound and distinct spectrographic qualities associated with F-20's howls. The resulting classification matrix is shown in Figure 3.9, with the standardized canonical discriminant function coefficients displayed in Table 3.8. The DFA performed using these select variables resulted in substantially improved discrimination between the SZ individuals, particularly coyote F-20. In fact, each of the three animals was classified in its own group membership category with the highest percent correct classification in this revised analysis.

Coyote (Sex-ID#)	*Group*	*Prior Probability*	*Actual C-V Classification*	*Difference*
M-1	BMZ	0.31	0.73	0.41
F-2		0.69	1.00	0.31
F-3	GZ	0.65	0.87	0.22
M-4		0.35	0.63	0.28
M-5	LD	0.52	0.54	0.02
M-6		0.48	0.68	0.20
F-7	MR	0.59	1.00	0.41
M-8		0.41	1.00	0.59
M-22	HNC	0.60	0.83	0.23
M-23		0.40	0.67	0.27
M-13	QZ	0.37	0.37	0.00
F-14		0.24	0.45	0.21
M-16		0.39	0.59	0.20
F-19	SZ	0.41	0.54	0.13
F-20		0.22	0.29	0.07
M-21		0.38	0.75	0.37

Table 3.6. DFA cross-validated classifications of individuals compared to prior (expected) probabilities in howl analyses.

	BMZ	**GZ**	**LD**	**MR**	**HNC**	**QZ**		**SZ**	
	Fn	Fn	Fn	Fn	Fn	Fn		Fn	
	1	1	1	1	1	1	2	1	2
PC1 (F0)	1.165	0.479	0.285	1.484	0.905	0.193	1.487	0.167	0.492
PC2 (Harmonics)	-0.134	-0.851	0.507	-1.385	-0.122	1.631	2.103	0.378	-0.419
PC3 (Duration)	0.661	0.878	0.479	-0.015	-0.002	-0.325	-1.383	0.284	0.799
PC4 (Begin Freq)	0.806	0.677	-0.073	1.232	-0.064	0.271	0.648	0.410	-0.135
PC5 (Shape)	0.551	0.367	-1.032	0.662	-0.140	0.726	0.768	-0.742	0.377
PC6 (Dom Freq)	-0.302	0.041	-0.162	-1.703	-0.139	0.345	0.975	0.336	0.312

Table 3.7. Combined matrix of howl data DFA standardized canonical discriminant function coefficients for all groups. (Gray-shading indicates that entire function was nonsignificant; aqua shading indicates that the function, when taken alone, was non-significant in discriminating among individuals.)

COY_ID	Predicted Group Membership			Total
	19.00	20.00	21.00	
19.00	7 (54%)	1 (8%)	5 (38%)	13
20.00	2 (33%)	3 (50%)	1 (17%)	6
21.00	4 (33%)	0 (0%)	8 (67%)	12

(a)

COY_ID	Prior Probability
19.00	0.419
20.00	0.194
21.00	0.387

(b)

Figure 3.9. Revised DFA for SZ group howls using select variables. (a) Cross-validated DFA classification matrix; (b) Prior (expected) probabilities by individual.

	SZ	
	Fn	
	1	2
logDFreq	-0.149	0.493
log_begf	1.438	-0.707
log_endf	0.030	-0.982
log_maxf	-1.401	0.434
log_minf	-0.021	0.111
MIN_T	0.227	0.345
MAX_T	-0.394	0.016
log_fund	0.387	1.300

Table 3.8. Standardized canonical discriminant function coefficients for revised SZ group DFA from howl data. (Aqua shading indicates that the function, when taken alone, was non-significant in discriminating among individuals.)

Temporal Qualities of the Chorus Howl Introduction

The temporal measurements of the howl vocalizations were examined to determine the pattern, if any, in which the coyotes entered the chorus. It was common that one individual would howl several times before other members of the group joined the chorus. These “introductory” howls were not included in the analyses presented here.

The chorus was considered to have begun when a howl was followed by a howl of a different individual.

Only the first two howls from each group member in a chorus were used for the following analyses, in order to best represent the introductory howling portion of the chorus as it has been described in the literature. Table 3.9 displays the mean interval between consecutive howl vocalizations within a chorus and the mean duration of the howl vocalizations produced by group members. The table also indicates the percentage of occurrences for which an individual initiated the chorus.

Captive Group	*Group Size*	*Number of Choruses (N)*	*Mean Interval Between Howl Begin Times (s)*	*Mean Duration of Howls (s)*	*% Occurrences of Individual (Sex-ID#) Initiating Chorus*
BMZ	2	4	2.17	2.29	F-2 (100%)
GZ	2	3	1.45	1.70	M-4 (67%) F-3 (33%)
HNC	2	5	2.50	2.49	M-23 (60%) M-22 (40%)
LD	2	9	1.08	1.62	M-5 (100%)
MR	2	4	1.56	0.97	F-7 (100%)
QZ	3	6	0.85	1.75	M-13 (50%) M-16 (33%) F-14 (17%)
SZ	5	3	1.67	2.19	F-20 (100%)

Table 3.9. Temporal qualities of chorus howl introduction.

As indicated by the mean interval times in Table 3.9, group members typically howl within 1 or 2 seconds of each other. Comparing the mean interval times with the mean howl durations, it appears that, with the exception of the MR group, the duration of howl vocalizations was greater than or equal to the time between howls, suggesting overlap between the howls of different group members.

Bark Variation Between Individuals

The PCA performed on the bark acoustic variables resulted in five principal components (PCs) with eigenvalues ≥0.95 (Tables 3.10 and 3.11). These five PCs accounted for 77.6% of the variance in the data set of 297 bark vocalizations from a total of 17 coyotes. Figure 3.10 shows the number of howls contributed per animal.

The five PCs were labeled based on factor loadings in the component matrix. The factor loadings for PC1 and PC2 were similar to those for the first two PCs in the howl PCA analysis. Therefore, these were similarly labeled, “F_0” (PC1) and “Harmonics” (PC2). However, the labeling for PC1 was based primarily on the five highest loading variables: the f_0, maximum frequency, ending frequency, minimum frequency, and beginning frequency. Again, as in the howl PCA, the lowest loading variables on PC1 were those related to the “shape” of the signal (the time of minimum frequency, MIN_T; and the time of maximum frequency, MAX_T). The harmonic-to-noise variable (logHNR) also had a very low loading (at 0.142). And although the highest loading components on PC2 were related to the higher harmonics of the signal structure, the harmonic peaks contributing to this PC were lower than those for the howl PCA, with the bark PC2 loading peaks 5 through 9, as opposed to the howl PCA loading peaks 6 through 10.

PC3 was labeled “Low Harmonics,” since the highest loading components were the frequencies of harmonic peaks 2, 3, and 4. However, these components were negatively correlated with PC3.

The bark PCA also resulted in a PC that was labeled “Shape,” based on the four highest loading components in PC4: time of maximum frequency, time of minimum frequency, and the beginning and minimum frequencies. The latter three of these components were negatively correlated with PC4.

As with the howl PCA, the last component, PC5, was most difficult to interpret and label. The highest loading components were various harmonic peaks, some positively and some negatively correlated with the PC. Therefore, PC5 was labeled “Varied Peaks.”

Total Variance Explained

	Initial Eigenvalues			Extraction Sums of Squared Loadings		
Component	Total	% of Variance	Cumulative %	Total	% of Variance	Cumulative %
1	5.320	29.557	29.557	5.320	29.557	29.557
2	4.062	22.565	52.123	4.062	22.565	52.123
3	2.069	11.496	63.619	2.069	11.496	63.619
4	1.549	8.604	72.224	1.549	8.604	72.224
5	.968	5.376	77.599	.968	5.376	77.599

Table 3.10. Total variance explained from PCA performed on bark data set, indicating five principal components extracted based on eigenvalues ≥0.95.

Component Matrix

	Component				
	1	2	3	4	5
logBegF	.761	-.493	.100	-.320	-.010
logEndF	.813	-.516	.056	.128	-.073
logMaxF	.813	-.529	.087	.038	-.032
logMinF	.780	-.486	.093	-.282	-.041
logFund	.816	-.511	.064	.046	-.007
logP1Frq	.446	-.238	-.080	.106	.183
logP2Frq	.414	.142	-.580	-.045	.473
logP3Frq	.400	.328	-.660	-.033	.307
logP4Frq	.456	.435	-.550	.025	-.078
logP5Frq	.527	.535	-.232	-.072	-.375
logP6Frq	.495	.651	.040	-.141	-.345
logP7Frq	.504	.677	.271	.016	-.162
logP8Frq	.487	.676	.350	.048	-.028
logP9Frq	.409	.606	.470	.131	.325
logP10Fr	.390	.518	.476	.143	.400
logHNR	-.142	-.343	.470	.144	.141
MIN_T	-.189	.105	.141	-.752	.156
MAX_T	.131	-.110	-.127	.824	-.078

Table 3.11. Component matrix from bark data PCA analysis. Values in columns headed Components 1 through 5 represent the correlation coefficients between the original variables (shown in the first column of the table) and the newly derived components.

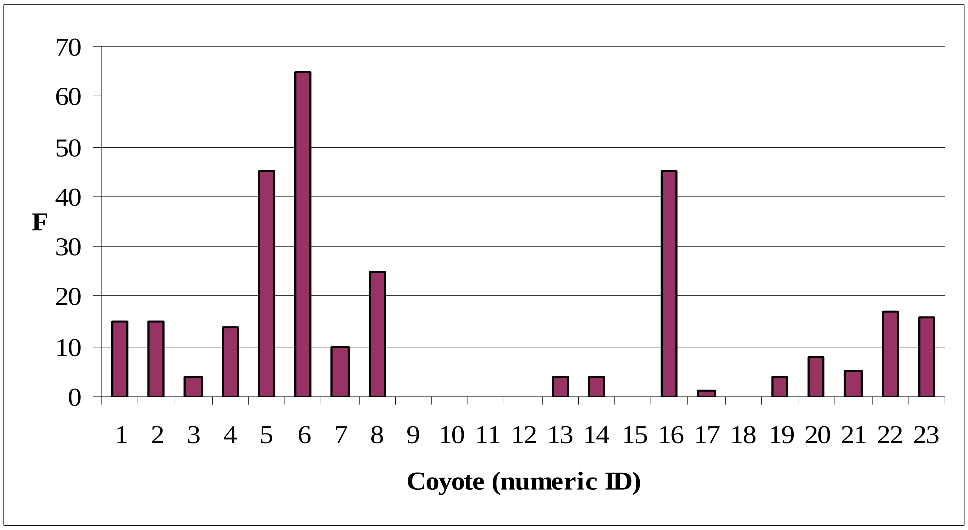
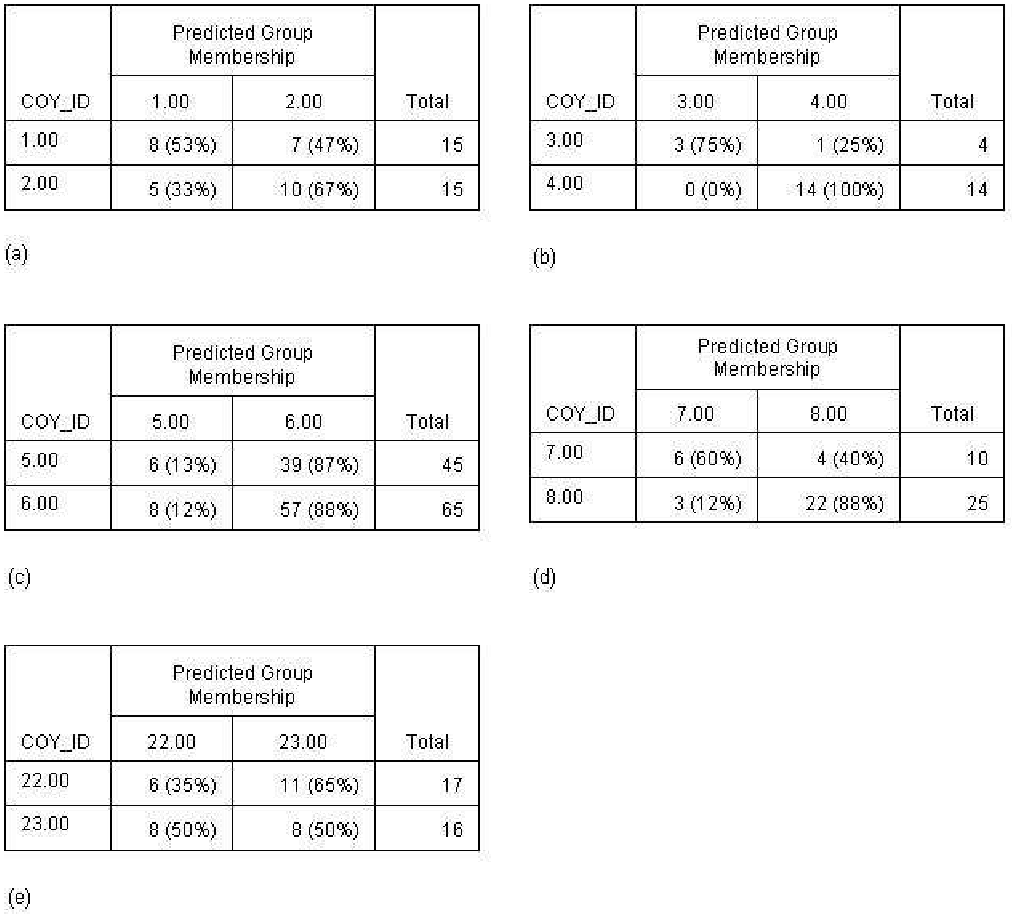


Figure 3.10. Number of barks per coyote contributed to PCA.

The DFA analyses on the zoo groups' bark vocalizations resulted in an average of 78.7% correct classification of individuals overall, with cross-validated DFAs resulting in an average correct classification of 63.5%. In total, 297 barks were classified from 17 coyotes, representing seven social groups. The classification tables in Figure 3.11 display the results of the cross-validated DFAs for each of the groups of two coyotes. The tables in Figure 3.12 display the results of the cross-validated DFAs for each of the groups in which the barks of three individuals were analyzed.



	Predicted Group Membership		
COY_ID	1.00	2.00	Total
1.00	8 (53%)	7 (47%)	15
2.00	5 (33%)	10 (67%)	15

(a)

	Predicted Group Membership		
COY_ID	3.00	4.00	Total
3.00	3 (75%)	1 (25%)	4
4.00	0 (0%)	14 (100%)	14

(b)

	Predicted Group Membership		
COY_ID	5.00	6.00	Total
5.00	6 (13%)	39 (87%)	45
6.00	8 (12%)	57 (88%)	65

(c)

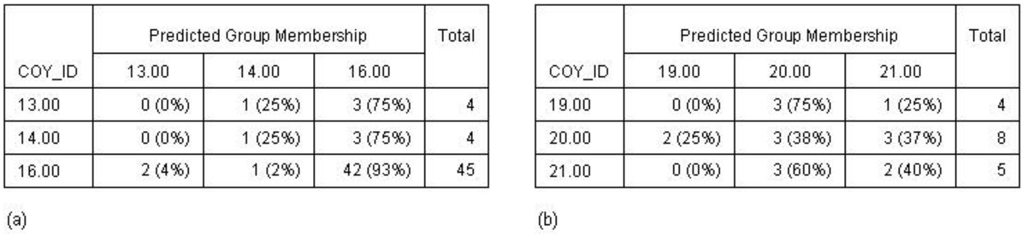
	Predicted Group Membership		
COY_ID	7.00	8.00	Total
7.00	6 (60%)	4 (40%)	10
8.00	3 (12%)	22 (88%)	25

(d)

	Predicted Group Membership		
COY_ID	22.00	23.00	Total
22.00	6 (35%)	11 (65%)	17
23.00	8 (50%)	8 (50%)	16

(e)

Figure 3.11. Classification results of cross-validated DFAs based on acoustic features of barks for coyotes within captive social groups of two animals. Tables represent captive groups: (a) BMZ; (b) GZ; (c) LD; (d) MR; (e) HNC.



COY_ID	Predicted Group Membership 13.00	14.00	16.00	Total
13.00	0 (0%)	1 (25%)	3 (75%)	4
14.00	0 (0%)	1 (25%)	3 (75%)	4
16.00	2 (4%)	1 (2%)	42 (93%)	45

(a)

COY_ID	Predicted Group Membership 19.00	20.00	21.00	Total
19.00	0 (0%)	3 (75%)	1 (25%)	4
20.00	2 (25%)	3 (38%)	3 (37%)	8
21.00	0 (0%)	3 (60%)	2 (40%)	5

(b)

Figure 3.12. Classification results of cross-validated DFAs based on acoustic features of barks for coyotes within captive social groups of ≥3 animals. Tables represent captive groups: (a) QZ and (b) SZ.

The DFAs on the bark data set revealed that the coyotes' barks within groups were much less discriminable than the howls analyzed above. Only three of the seven groups' discriminant functions were significant (Wilks' lambda, $p < .05$). These were the GZ, MR, and QZ groups. The prior (expected) probabilities versus the actual cross-validated classification proportions for each animal are shown in Table 3.12.

Coyote (Sex-ID#)	*Group*	*Prior Probability*	*Actual C-V Classification*	*Difference*
M-1	BMZ	0.50	0.53	0.03
F-2		0.50	0.67	0.17
F-3	GZ	0.22	0.75	0.53
M-4		0.78	1.00	0.22
M-5	LD	0.41	0.13	-0.28
M-6		0.59	0.88	0.29
F-7	MR	0.29	0.60	0.31
M-8		0.71	0.88	0.17
M-22	HNC	0.52	0.35	-0.16
M-23		0.49	0.50	0.01
M-13	QZ	0.08	0.00	-0.08
F-14		0.08	0.25	0.18
M-16		0.85	0.93	0.08
F-19	SZ	0.24	0.00	-0.24
F-20		0.47	0.38	-0.10
M-21		0.29	0.40	0.11

Table 3.12. DFA cross-validated classifications of individuals compared to prior (expected) probabilities in bark analyses.

The standardized canonical discriminant function coefficients for the three significant DFAs suggested that harmonic structure was the most important acoustic feature contributing to the discrimination between individuals' barks (Table 3.13). This may not seem surprising, since four of the five PCs entered into the DFAs were labeled as harmonic components. However, it seems noteworthy that at least two components associated with harmonic peaks (e.g., those PCs labeled harmonics, low harmonics, and varied peaks) had higher discriminant loadings than the fundamental frequency component in each of these three DFAs, suggesting that some feature(s) of the harmonic structure were useful in discriminating between individuals and that this discrimination was not necessarily based on the harmonics' relationship to the f_0.

	GZ	**MR**	**QZ**	
	Fn	Fn	Fn	
	1	1	1	2
PC1 (F0)	-0.534	0.906	0.285	-1.711
PC2 (Harmonics)	2.097	1.794	-0.990	-1.608
PC3 (Low Harmonics)	-0.126	1.497	0.770	1.255
PC4 (Shape)	-0.348	1.247	-0.583	0.496
PC5 (Varied Peaks)	1.611	0.166	0.638	2.314

Table 3.13. Combined matrix of bark data DFA standardized canonical discriminant function coefficients for groups with significant DFs. (Aqua shading indicates that the function, when taken alone, was non-significant in discriminating among individuals.)

Chorus Duration

To test whether differences in chorus duration existed between different-sized groups of individuals, the mean chorus lengths from each of the seven captive groups were compared. A one-way ANOVA indicated an overall difference ($p = 0.032$), with

Tukey HSD post hoc comparisons revealing that there were significant differences between the chorus lengths of the HNC and BMZ groups (p = 0.018) and the HNC and LD groups (p = 0.044). However, these three groups each contained only two vocalizing individuals. In addition, there were no apparent trends in chorus duration related to group size (Figure 3.13).

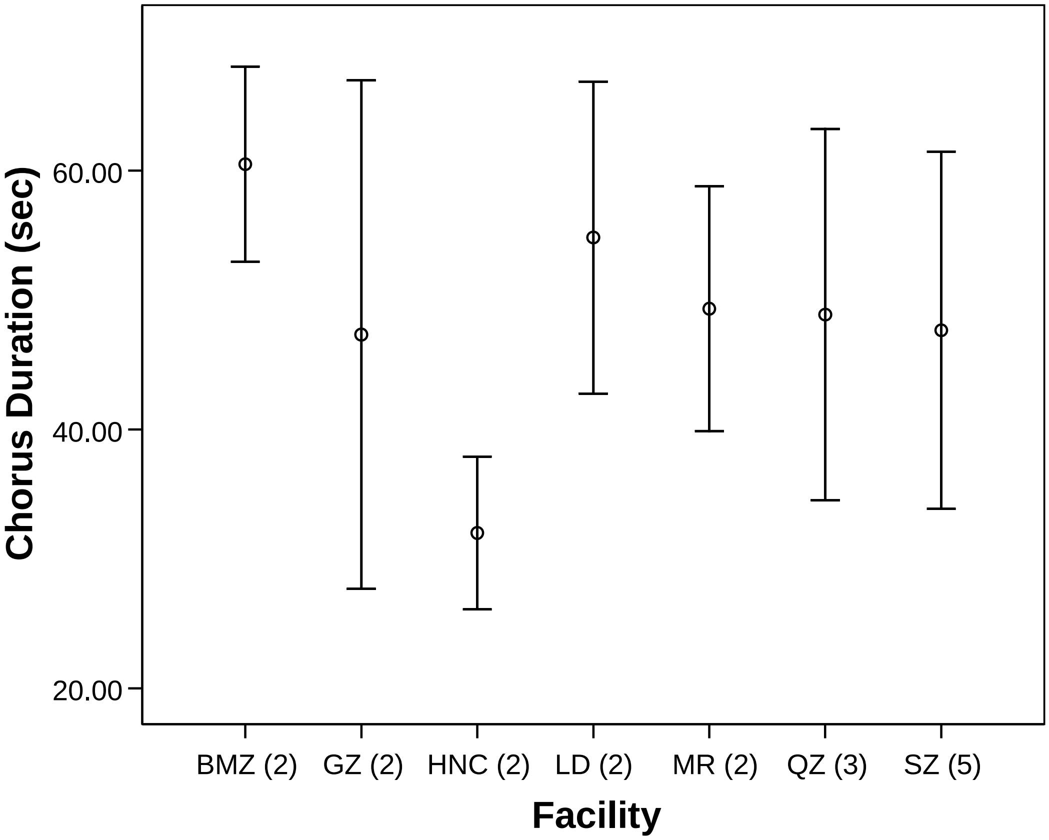


Figure 3.13. Mean chorus durations for seven captive groups of coyotes. Numbers in parentheses beside facility abbreviations on x-axis represent group size. (Error bars indicate one standard deviation from mean.)

Human Estimates of Group Size

Participants in the coyote group-size estimation exercise varied in their ability to estimate the number of animals vocalizing in the recorded segments of yip-howling choruses. However, none of the participants provided correct estimates for all six segments. Fifty-two percent of the human subjects correctly estimated the number of animals in only one (17% correct) or none of the segments. Nineteen percent provided correct estimates for two of the segments (33%), 14.3% correctly estimated three segments (50%), and 14.3% correctly estimated four segments (67%). Although estimates were frequently incorrect, they were within a reasonable range from the actual group size, as Figure 3.14 indicates. Overall, 32% of human subjects correctly estimated the group size from the INTRO segments and 27% correctly estimated from the YIP segments.

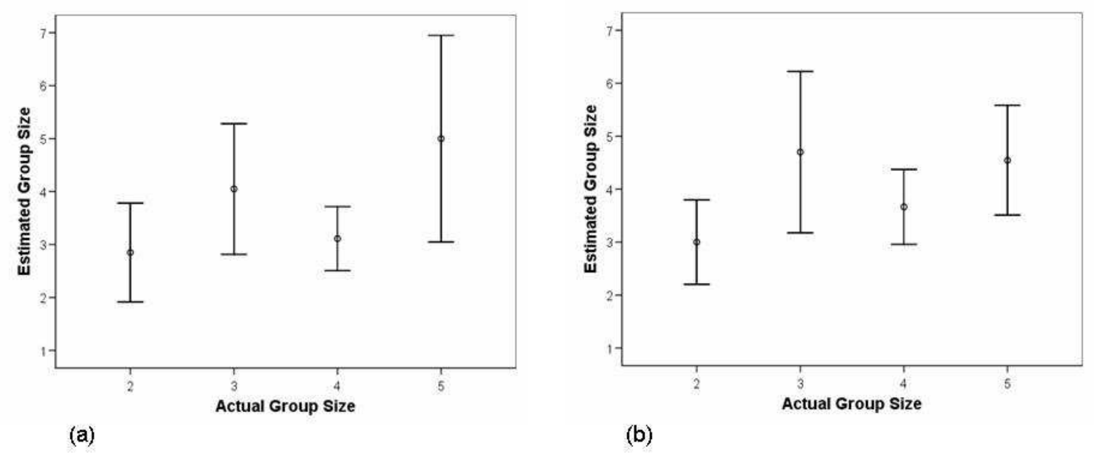


Figure 3.14. Human estimates of coyote group size based on segments of recorded group yip-howl choruses. a) Estimates based on INTRO section of chorus; b) Estimates based on YIP section of chorus. (Error bars indicate one standard deviation from mean.)

The perceptual cues used by the subjects in determining group size estimates were similar across subjects and were placed into five classification categories by the researcher: voice, timing, combined voice/timing, rhythm, and amplitude. Voice cues were those that allowed for recognition of individual voices by frequency (pitch) or a characteristic style of vocalizing. Timing cues were related to the entry of voices into the chorus and the onset and offset of individual vocalizations. Cues categorized as combined voice/timing were those described by participants as different vocalizations occurring simultaneously or alternating vocalizations, in which the human subject could identify one individual's voice "answering" another's. Rhythm cues referred to the cadence of a vocalization, such as an individual barking repetitiously at a constant time interval. Amplitude was the least commonly cited of the five cue types, but was specifically referred to by 11 of the participants as a means of estimating the number of vocalizing animals.

Voice and combined voice/timing cues were used equally in attempting to determine group size from INTRO and YIP segments of a chorus, with these cues referenced in 72.7% of the participants' comments for the INTRO portion and 72.2% of their comments for the YIP portion. However, timing cues were significantly more important in the howl-dominated INTRO segments than in the YIP segments, making up 25.3% of the total participants' comments for INTROS and only 4.6% for YIPS. Conversely, rhythm was never indicated as a cue to group size for INTRO segments, but made up 15.7% of the participant comments for YIP segments. Participants also seemed to draw on amplitude cues more frequently for YIP segments than for INTRO segments (7.4% and 3.0%, respectively).

Discussion

Prior studies investigating the potential of group-living animals to assess the fighting ability of conspecific groups through long-distance vocal signals have measured the movement and vocal responses of territory-holding residents to playbacks of conspecific group vocalizations (Kitchen, 2004; McComb et al., 1994; Radford, 2003; Wilson et al., 2001). However, none of these studies has analyzed the vocal signal itself to determine whether there are acoustic features of the signal that could provide information about group size.

The acoustic analyses conducted in the present study support the hypothesis that group size information is potentially available in the group yip-howl vocalization of the coyote. Both the introductory howl component of the signal and the more variable yipping portion of the vocalization were analyzed. These analyses revealed that, within a social group, individual animals' howls were largely discriminable, potentially allowing them to be "heard out" and "counted." Howls were more easily assigned to individual animals than were barks, based on the acoustic features measured for each, suggesting that the howl-dominated introductory section of the chorus might contain more information about group size. Six of the seven (86%) discriminant functions (DFs) in the howl analyses were significant, indicating that they were capable of effectively discriminating between individuals; whereas only three of the seven (43%) DFs were significant in the bark analyses.

When talking with people in the general public about coyote observations, it was common for the researcher to be told of large coyote groups (of 10 or more individuals) heard vocalizing in the area. This overestimation could be due to the greater salience of the yip section when heard by humans in a natural setting. Although the howls propagate well through the environment, they can often be mistaken for other environmental sounds (e.g., distant police sirens) and, therefore, are largely ignored by people. It seems that human attention turns to the signal when the more unusual, clearly recognizable yip section of the chorus is heard, resulting in an overestimation of group size. Coyotes are much less likely to ignore the initial howl stimulus, as was observed by the researcher during playbacks of chorus howls to captive groups of coyotes. From the start of the first howl of the playback, the animals oriented toward the sound, often moving to the area of their enclosure closest to the sound source, while carefully attending to the signal (as indicated by body posture and ear position).

Although human subjects were not precisely correct in their estimations of group size based on the chorus howl segments they heard, their estimates were much closer to the actual number than was expected based on accounts provided by the public, as described above. In fact, the mean estimates were within one or two of the actual numbers. These results suggest that people can assess coyote group size fairly accurately from a group yip-howl chorus. This finding could have practical implications for censusing coyote populations.

The results of the acoustic analyses and the human perceptual task suggest that individual voice characteristics (e.g., f_0 and harmonic structure) are important cues for discriminating between individuals in a chorus. Participants in the perceptual task also commented frequently on the importance of overlap of vocalizations in determining the number of animals present. The howl interval data suggested that howls commonly overlap during the introductory portion of the chorus, but with voice onset occurring at different times. Such characteristics clearly indicate that more than one animal is vocalizing (McComb et al., 1994).

Of course, it is impossible to perfectly characterize a complex sound through acoustic measurements. The example of the unique voice characteristics of the coyote in the SZ group not being discriminated in the original acoustic analyses highlights the problems inherent in such studies. However, the human perceptual task supported the statistical results indicating that group size is discernable in the chorus howl of coyotes. Perhaps future studies can further isolate the acoustic features that make this discrimination possible.

Two previously held beliefs about canid chorus vocalizations were not supported by this study. It has been suggested that the alpha male, or one of the animals of the alpha pair, initiates the chorus howl in wolves (Harrington and Mech, 1979). Although this might be assumed to be the case for the captive male-female pairs in the present study, the results from one of the male-male dyads and the two larger groups are ambiguous. Both males started howls in the dyad and all three animals (2 males and 1 female) each started howls in the captive group at Queens Zoo. In the group at Stone

Zoo, the lowest ranking female of that sibling group of five started all the howl choruses. However, due to the unnatural setting and often artificial groupings of animals in these captive environments, extrapolation to the behavior of wild groups is problematic.

It has also been suggested that group vocalizations might serve to inflate the perceived number of individuals vocalizing. Harrington (1989) suggested that the Beau Geste effect applies to wolf chorus howling. The Beau Geste hypothesis argues that resident animals deceive potential intruders into believing that there are more territory owners than there actually are, thereby discouraging the intruders from entering into conflict with the resident group. Harrington based this argument on his perception that researchers were unable to identify the number of wolves howling in a chorus. However, he provided no empirical evidence that this was true or that wolves were unable to perceive the correct number of individuals. On average, the human subjects in the present study closely estimated the number of individuals participating in the howling introduction of a coyote group yip-howl. The introductory howling in this coyote group vocalization is most similar to howling choruses produced by wolves.

Radford (2003) found that spontaneous group vocalizations of green woodhoopoes honestly represent group size in the duration of the signal. However, upon hearing calls of a larger group, a smaller group will increase the length of its vocal bout to match that of the competing group. Although such a matching effect was not tested in the study presented here, the duration of the coyote group yip-howls were not correlated with group size.

CHAPTER 4

RESPONSES OF RADIO-COLLARED COYOTES TO CHORUS HOWL PLAYBACKS OF DIFFERENT-SIZED GROUPS

Introduction

Game-theoretical models of agonistic behavior suggest that animals should base decisions about conflict escalation on an assessment of their opponent’s fighting ability or resource-holding potential (RHP). A multitude of asymmetries can exist between individuals competing for possession of resources, including size and strength of each individual, current ownership of the resource, and the importance of the resource to each competitor. In competitions where fighting is costly, it is selectively advantageous for an animal to assess its chances of winning and withdraw without escalation if those chances are low (Enquist & Leimar, 1983; Hammerstein, 1981; Maynard Smith, 1982; Maynard Smith & Parker, 1976; Parker, 1974).

Aggressive displays, including some vocalizations, are believed to function as advertisements of an animal’s fighting ability or resource-holding potential (RHP), allowing a competitor to assess its chance of winning in a direct conflict (Clutton-Brock & Albon, 1979; Parker, 1974). Studies of such advertisement displays have typically focused on contests between individuals. It is believed that in these contests the assessment criteria are closely linked with the individual's RHP or fighting ability (Clutton-Brock & Albon, 1979). Some suggested criteria in these one-on-one contests include the size of potential "weapons," such as antlers and canines (Darwin, 1850; Geist, 1971; Packer, 1977); the pitch of a vocalization, with lower pitch indicating larger body size (Morton, 1977); and the frequency and duration of a physical or vocal display, with longer or more frequent displays indicating better condition (Clutton-Brock & Albon, 1979).

By similar reasoning, it might be expected that correct assessment of group size would be an important criterion in determining potential costs in contests between groups of animals. Social animals would benefit from accurate perception of group size when assessing the fighting ability or RHP of a competing group in the same way that individual competitors benefit from assessment of their single competitor's size and strength (McComb et al., 1994).

Gese (2001) suggested that howling might serve as a long-range threat in the maintenance of resident coyotes' territories, repelling potential intruders at a distance. Coyotes are considered to be territorial when in a bonded pair or pack social configuration (Messier & Barrette, 1982; Windberg & Knowlton, 1988). Coyotes in these social groups, referred to as residents, often traverse home ranges larger than 20 km^2 for activities such as foraging. These ranges typically overlap substantially with ranges of neighboring resident coyotes, as well as transient animals. However, resident coyotes spend a good portion of their time in smaller areas within these ranges, often referred to as core areas or territories. These territories do not overlap with those of other coyote groups and contain important resources, such as protective cover and den sites (Bekoff & Wells, 1980; Laundré & Keller, 1984; Gese et al., 1988; Person & Hirth, 1991). These areas are vigorously defended by resident animals (Gese, 2001).

Among the Canidae, playback experiments have been used to study howling behavior in coyotes, wolves, and jackals. Playback experiments typically involve playing back a recording of a species-typical acoustic signal to an animal and measuring its response. This method has played an instrumental role in studies of mating and territorial strategies in song birds and has elucidated the role song plays in these and other aspects of passerine life (Falls, 1992). Early studies with wolves employed playback recordings and human imitations of howls to locate and maintain contact with study animals (Joslin, 1967; Theberge & Pimlott, 1969). Harrington (1987) used playbacks to study the role of howling during aggressive encounters in wolves and the wolf's perception of and response to howling by adults versus pups (1986). In coyotes, Lehner (1982) investigated the potential functions of two different types of howling choruses, and Mitchell (2004) explored the possibility of using howling playback as a tool for selective coyote control. Seasonal changes in howling behavior and the relationship between howling and confrontation in the golden jackal were studied by Jaeger et al. (1996). In each of these studies, howling was considered to play an important role in the territorial strategies of these species.

In the study presented here, playback experiments were employed to further investigate the function of chorus howling in coyote territorial strategy. It was predicted that playback of chorus howls produced by small groups of coyotes would result in a significantly larger number of approaches to the stimulus than would playback of large-group choruses. This prediction was based on models of agonistic competitor assessment (Enquist & Leimar, 1983) and the assumption that coyotes in human-populated areas do not typically form large adult groups. Packs of adult coyotes typically consist of a resident pair (the alpha pair) and their offspring.

Experiments were conducted with radio-collared coyotes in agricultural and agricultural-suburban landscapes in central Ohio and the forest preserves and western suburbs of Chicago, Illinois. Individual radio-collared animals were tested with two experimental conditions: 1) the PAIR condition, in which a group yip-howl (GYH) produced by two coyotes was used as the playback stimulus; and 2) the PACK condition, in which the playback stimulus was a GYH of a group of five coyotes. The movement of the target animals and their vocal responses were recorded.

Methods

Subjects

Individuals from two populations of radio-collared coyotes were the subjects in this study. One population was located in central Ohio and consisted of animals radio-collared between December 2003 and March 2006. That population and the procedures used to collar and radio-track them are described in Chapter 3. The second population was located in Cook and Kane Counties west of Chicago, Illinois. These coyotes were radio-collared as part of a larger, ongoing study being conducted by Dr. Stanley D. Gehrt

(School of Environment and Natural Resources, The Ohio State University), The Max McGraw Wildlife Foundation, and the Cook County Division of Wildlife.

Data from playback studies with eight coyotes from the Ohio population (5 females, 3 males) and eleven coyotes from the Illinois population (5 females, 6 males) were analyzed for this study. These nineteen animals represented coyotes considered to be resident animals holding a defended territory. Only one animal from any given social group was radio-collared in the Ohio population; therefore, it was not known whether these animals were with others at the time of the playback unless there was a vocal response produced by multiple animals. Several animals in some groups in the Illinois population were radio-collared, with family relationships known in some cases from pit-tagging and subsequently collaring pups found in dens of collared adults and/or from DNA analyses. When individuals from these groups were targets in playback trials, they were often known to be with other group members. However, only the data for the target animal were used in comparative analyses. In addition, only data from one individual in a group were collected within an annual season.

Playback Stimuli

Recordings collected from captive facilities (described in Chapter 2), as well as recordings from other researchers, were used as playback stimuli for the present study. Recordings consisted of a group yip-howl chorus of either two (PAIR condition) or five (PACK condition) coyotes. Although original recordings of coyote howling choruses were preferred, a limited number of these recordings were available for the PACK condition stimuli. Only one of the captive groups recorded by the researcher and one group recording obtained from the British Library National Sound Archive consisted of five coyotes. Therefore, additional PACK condition stimuli were created by combining recordings from coyote groups of two and three. This technique has been used in similar studies by Kitchen (2004) and McComb et al. (1994).

Eleven different recordings, recorded from four male-female coyote pairs, were used as pair-condition stimuli. Recordings from the same pair were collected during separate howling bouts and, therefore, varied in structure and duration. There were four recordings from one captive pair, three recordings each from one captive and one wild pair, and one recording from another captive pair. One of these recordings was used in three separate trials; six recordings were used in two trials; and four recordings were used in only one trial. Thirteen recordings, representing two “natural” and five “digitally-created” mixed-sex groups, were used as PACK-condition stimuli. There were six recordings from one captive group, one recording from one wild group, and six digitally-created recordings. As with the PAIR recordings, the six recordings from the one captive group were collected during separate howling bouts. Six of these recordings were used in two trials and the other seven were used in only one trial.

Playback recordings varied in length from 30 to 70 seconds. PAIR- and PACK-condition stimuli lengths were matched for each target subject and order of condition presentation was varied randomly across subjects. Playback stimuli were played at an average peak volume of 80 dB SPL (range: 75 – 86 dB SPL), as measured at 1 m from the source by a digital sound level meter (Radio Shack) using C frequency weighting. Speaker (Nagra DSM Monitor) volume was adjusted for each playback based on settings determined prior to the experiments using a sound amplitude meter. PAIR and PACK stimuli for each target animal and for target animals from the same social group consisted of recordings of different coyote groups (i.e., recordings from the same captive group were not used in both conditions of the experiment for a particular target animal or target animals from any given social group). The average interval between tests of different target animals in the same social group was 14.8 days (range: 1.4 – 35 days; median = 10).

Playback Experiment Procedure

Playback trials were conducted between March and May in 2004, 2005, and 2006. The trials used for analyses were those conducted with resident animals for which sufficient data were collected (e.g., continuous radio-collar signal strength recorded with the datalogging receiver). Trials were conducted between the hours of 22:00 and 05:00. Since the radio-collared coyotes ranged in human-populated areas, playback experiments could only be conducted when human activity levels were low. The average number of days between experimental conditions for a target animal was 28.9 (range: 12 – 63; median = 25) in Ohio and 13.8 (range: 1.4 – 35; median = 10) in Illinois.

In 2004, trials were conducted using only the Ohio population of radio-collared coyotes. During this year's trials, playback stimuli were played from a portable CD player through a speaker mounted in a side window of the research vehicle. Four 4-element Yagi antennas were mounted on top of the vehicle, facing perpendicular to one another, and connected to a datalogging receiver (LOTEK SRX-400) (Figure 4.1). The radio-collared animal's movement toward or away from the vehicle, as well as its directional movement, could be measured with this antenna array. A research assistant stayed in the research vehicle and controlled playback using the CD player, while the researcher drove in another vehicle to a location several hundred meters from the playback site to monitor the target animal's movements using a handheld telemetry system. The playback stimulus was presented 15 minutes after setup was complete and the researcher had left for the monitoring site. Both vehicles remained in position for at least 30 minutes after the playback had been presented. After this time, the researcher returned to the playback site, the equipment was dismantled, and the research team left the location.

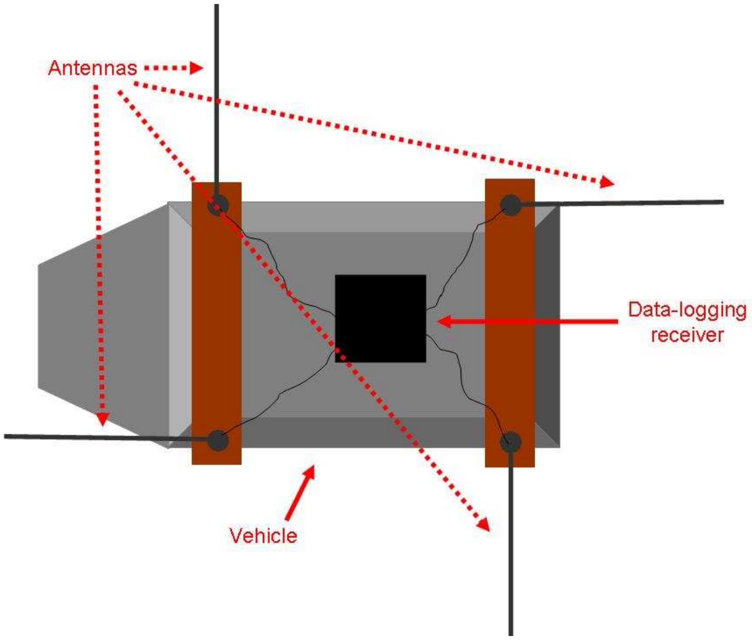


Figure 4.1. Schematic of research vehicle (as viewed from overhead) with mounted antenna array used in 2004 playback experiments to record target animals' movements.

The experimental procedure was modified for the 2005 and 2006 trials. An autonomous playback apparatus (Figure 4.2) was constructed of a 66 X 47 X 42 cm crate mounted on a 28 cm-high platform. The entire apparatus was covered in camouflage-colored burlap. A portable CD player and the datalogging receiver were placed inside the crate. A speaker, connected to the CD player, and an omnidirectional magnetic-mount whip antenna, connected to the receiver, were placed on top of the crate. A directional microphone (Audiotechnica 815A), housed inside a wind muff, and a cassette tape recorder were placed alongside the apparatus. The CD contained two tracks: the first was a silent 10-minute segment and the second was the playback recording. The silent track allowed for a 10-minute pre-trial period to begin after the apparatus had been set up and the research team had left the area.

Figure 4.2. Autonomous playback apparatus used in 2005 and 2006 trials with radio-collared coyotes in Ohio and Illinois.

Due to the unpredictable travel patterns of coyotes during the hours in which trials were conducted, the decision to test any given animal on a particular night was determined by the animal's location and the ability of the research team to get the playback apparatus within close enough range to ensure that the animal would hear the playback stimulus and the datalogger would record the signal strength of the radio-collar beacon. Typically, the criterion was that the datalogger was registering the collar signal strength near 100 (maximum strength = 235) with the receiver's gain set between 65 and 80. Based on tests of the datalogger, the animal was presumed to be within 200 – 300 meters of the apparatus using this criterion. This distance can only be estimated, as signal strength is dependent on many environmental factors (e.g., vegetation, topography, humidity, wind) and the strength of the individual radio-collar's transmitter.

All trials except one were conducted when the target animal was within its home range, defined as the 95% utilization distribution (UD) and considered to be the area regularly traversed by the animal during normal activity (e.g., feeding). Home ranges were calculated using the fixed kernel method, as described in Chapter 2. After locating the animal using vehicle-based radio telemetry and determining that the animal was within the criterion range, we placed the playback apparatus at a site that would allow for the best transmission of the playback recording through the environment (e.g., at the top of an embankment) and which, we hoped, was visually hidden from the target animal. As the coyotes were often moving, the equipment needed to be set up as expeditiously as possible, without creating a great deal of disturbance in the area that could draw the animal's attention. After setting up the autonomous playback apparatus, the research team left the playback site and drove to a location from which they could monitor the animal's movement, when possible, without interfering with the trial. Approximately 30 minutes after the playback stimulus had been presented, the research team returned to the playback site, retrieved the apparatus, and left the location.

Data Analyses

Signal strength data was downloaded onto a computer from the datalogging receiver's "Event Log" program. During the playback trial (pre-trial, playback, and post-trial), Event Log scanned through all radio-collar frequencies in a user-defined partition of the program. If only one animal was in the vicinity at the time of the trial, then only that animal's collar frequency was entered into the partition. In Illinois, if any other radio-collared group members were in the vicinity of the target animal, their collar frequencies were also entered into the partition. Event Log scanned each frequency for six seconds before cycling through to the next frequency in the partition and stored the time, date, pulse rate, and signal strength for each collar frequency it detected. In addition, Event Log scanned each of the four antennas in the array in the 2004 Ohio trials, registering each antenna's received signal strength and calculating an average from these four readings for each scan. Only the averaged data were used for analyses.

The data (time and signal strength) collected for the target animal were divided into two time periods: 5-minute pre-trial and 5-minute post-trial. These time periods were relative to the start time of the playback stimulus, with the 5-minute post-trial period starting at the playback start time. The mean signal strength for each time period was entered as a variable into the SPSS statistical software program for each playback condition for each target animal. Five-minute pre-trial and 5-minute post-trial means were compared, within animals, for the PAIR and PACK conditions using a Wilcoxon signed ranks test.

Various conditions are believed to affect coyote responses to conspecific vocalizations. These include the season (Gese & Ruff, 1998; Laundré, 1981; Walsh & Inglis, 1989), the location of the target animal within its home range (Gese & Ruff, 1998), and whether the target animal is alone or with others (P. N. Lehner, personal communication, March 4, 2004). All data from the playback trials conducted in this study were coded to identify these potential confounding variables as follows:

1. Season: The annual season in which the trial was conducted.
2. Territory: The area in the target animal's range in which the trial was conducted.
3. Social: Whether the target animal was known to be alone or with other pack members at the time of the trial.

Chi-square tests were performed to determine whether bias existed in the data set that could affect the results of the PAIR-PACK condition comparisons. All playback trials were conducted between March and May; therefore, the "Season" variable was split into two seasons: BREEDING/GESTATION (January – April) and PUP-REARING (May – August). The "Territory" variable was used to define whether the animal was in or near its core (50% UD) territory. When multiple 50% UD contours were calculated for animals with known, radio-collared mates, the animal's core territory was considered to be only within contours which overlapped with the 50% UD contours of its mate. The animals' locations were plotted on UTM-projected digital maps in ArcView. The Territory variable was split into two conditions: OUTSIDE when the animal was estimated to be outside the core area's contour, and INSIDE when the animal's location was estimated to fall within the contour.

Similarly, the "Social" variable was split into two conditions: OTHERS when another radio-collared group member's beacon was registering during the playback trial, and ALONE when an animal whose known mate was radio-collared and that animal's beacon was not registering during the trial. Whether the animal was alone or with other group members was unknown for eight of the PACK trials and seven of the PAIR trials. Therefore, it was decided to split these trials between the OTHERS and ALONE conditions. Four of the PACK trials were placed in the OTHERS condition and four were placed in the ALONE condition. For the seven PAIR trials, a coin flip decided that four of those trials would be placed in the ALONE condition with the other three placed in the OTHERS condition.

Animal home ranges (95% UD) and core territories (50% UD) were determined using fixed kernel analysis. Location data from September of the previous year through August of the year of the trial were used in these calculations for the 2004 and 2005 seasons for both the Illinois and Ohio coyote populations, and for the 2006 season for the Ohio coyotes. The 2006 UDs for the Illinois coyotes were based on location data from September 2005 through March 2006. The position of the target animal during the playback trial was estimated from its signal strength and direction relative to the playback apparatus at the time of set up, as determined using a handheld radio receiver and a 3- or 4-element Yagi antenna.

Results

Movement Responses to Playback

The coyotes' movement responses to playbacks, based on radio-collar signal strength, were compared between the PAIR and PACK stimulus conditions. The difference in mean signal strength between the 5-minute pre-trial and 5-minute post-trial was compared between the PAIR and PACK conditions. A Wilcoxon signed ranks test indicated that the animals responded significantly differently to the two playback conditions (T+ = 13, N = 19, p = 0.033). As Figure 4.3 illustrates, the coyotes more frequently moved toward the PAIR playback than the PACK playback. In addition, the magnitude of their movements was greater in the PAIR condition. Conversely, the magnitude of the animals' movements was relatively small in response to the PACK stimuli, and the animals most frequently moved away from the playback source.

Although sample sizes were small, this pattern of movement (away from PACK and toward PAIR playbacks) was examined further within the "Territory" and "Social" variables. Coyotes typically moved away from PACK playbacks, regardless of their location in their home range or whether or not they were with other animals at the time of the playback. Out of eight trials in which residents were in their core territories at the time of a PACK playback, seven resulted in movement away from the stimulus. When outside their core territory, animals moved away from the stimulus in six out of nine

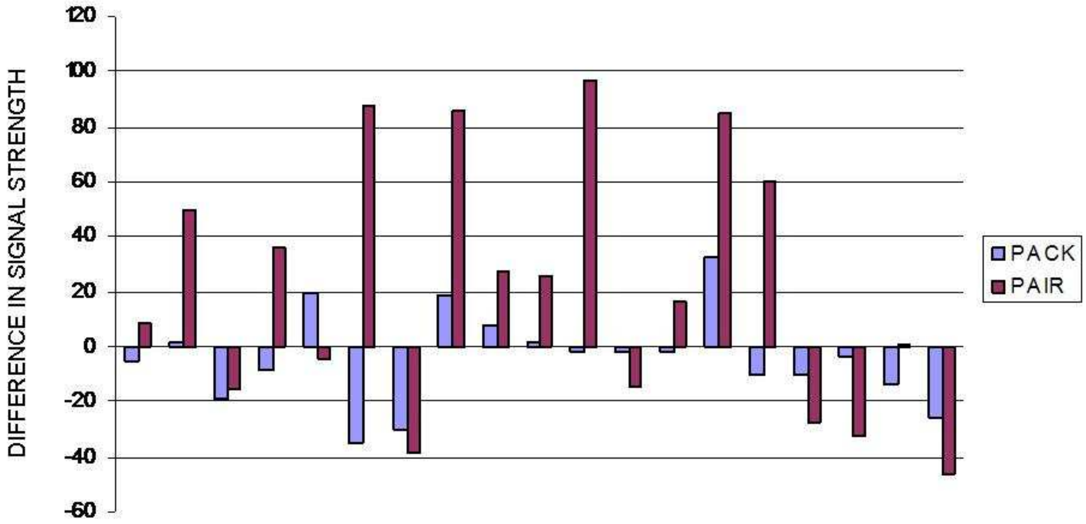


Figure 4.3. Individual coyote's movement responses to PACK and PAIR playback stimuli. Bars represent the difference in mean signal strength between the 5-minute pre-trial and 5-minute post-trial periods. Longer bars represent larger movements toward (above zero) or away from (below zero) the playback stimulus.

trials. Target animals also moved away from the PACK stimulus when they were believed to be alone (5/8 trials) and when they were with other group members (8/9 trials). However, resident coyotes tended to approach PAIR playbacks when inside their core territories (6/9 trials) and when they were with other group members (7/11 trials). When possibly alone or outside their core territories, animals moved away from the PAIR stimulus during half the trials and moved toward it during the other half. Unfortunately, sample sizes were not large enough to analyze interactions between the territory and social configuration variables.

Possible Confounding Variables

Chi-square tests on the possible confounding variables (Season, Territory, and Social) indicated that there were no systematic differences in these variables between the

PAIR and PACK conditions of the playback trials (Figure 4.4). For all three variables, there were 19 PAIR- and PACK-condition trials compared (N=19). For the Season variable, an equal number of PACK- and PAIR-condition trials were conducted in the breeding/ gestation period and in the pup-rearing season (χ2 = 0.00, df = 1, p = 1.00). There were also an equal number of PACK- and PAIR-condition trials conducted when the target animal was inside and outside its core territory (χ2 = 0.00, df = 1, p = 1.00). Trials conducted when the target animal was alone did not differ between the two playback-trial conditions, with 9 target animals being categorized as “alone” in PACK-condition trials versus 7 in PAIR condition trials (χ2 = 0.432, df = 1, p = 0.511). Again, some of these were categorized without actual knowledge of social status, as only the target animal was collared.

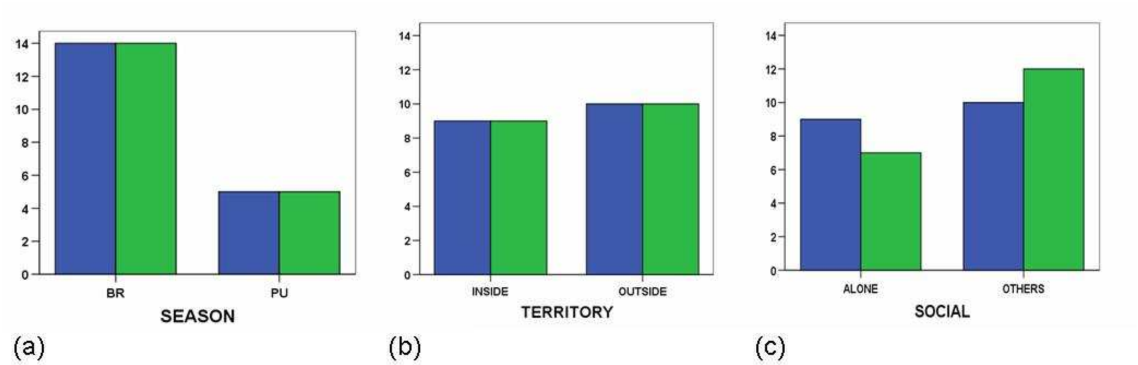


Figure 4.4. Bar graphs showing the number of trials conducted within different a) seasons, b) home range areas, and c) social configurations. Experimental conditions are shown with blue (PACK) and green (PAIR) bars.

Vocal Responses to Playback

Vocal responses from wild coyotes were recorded during six of the playback trials, three in Ohio and three in Illinois. All vocal bouts occurred after the playback stimulus had been presented. Five responses occurred during the 5-minute post-trial period and one occurred in the 5-to-10-minute post-trial period. Responses were assumed to be from the target animal and/or members of its social group, as the vocalizations were judged by the research team to be coming from the area of the target animal's estimated location. This method of judging response was also used by Okoniewski & Chambers (1984). Vocal bouts that occurred within the 5-minute post-trial period were assumed to be responses to the playback stimuli.

Group yip-howls were recorded during four trials, and all occurred within the 5-minute post-trial period. Three of these howling choruses were in response to PAIR playback stimuli and one was in response to a PACK playback stimulus. Only the response to the PACK stimulus began while the playback stimulus was still sounding. Due to the microphone's close proximity to the playback speaker, the start time of the response could not be distinguished in the recording; however, the vocal response continued for 50 seconds after the playback stimulus ended. In the three PAIR-condition trials, latencies from the end of the playback stimulus to the start of the chorus howl response were 0:25, 1:03, and 4:14 (min:sec). The durations of these three group yip-howls were 1:07, 0:55, and 0:43, respectively.

Although the logged radio-collar signal strength indicated that the target animal approached the playback apparatus in each instance that a group yip-howl response was recorded, the timing of the approach varied between trials, with no clear pattern emerging (Figure 4.5). In each of the trials in which a group yip-howl response was recorded, the target animal appeared to be within its core (50% UD) area. Again, the target animals' locations were estimated by direction and signal strength using a radio-receiver and Yagi antenna while the research team was setting up the playback apparatus. The locations of the target animals and playback apparatus during the setup period for these trials are shown in Figure 4.6.

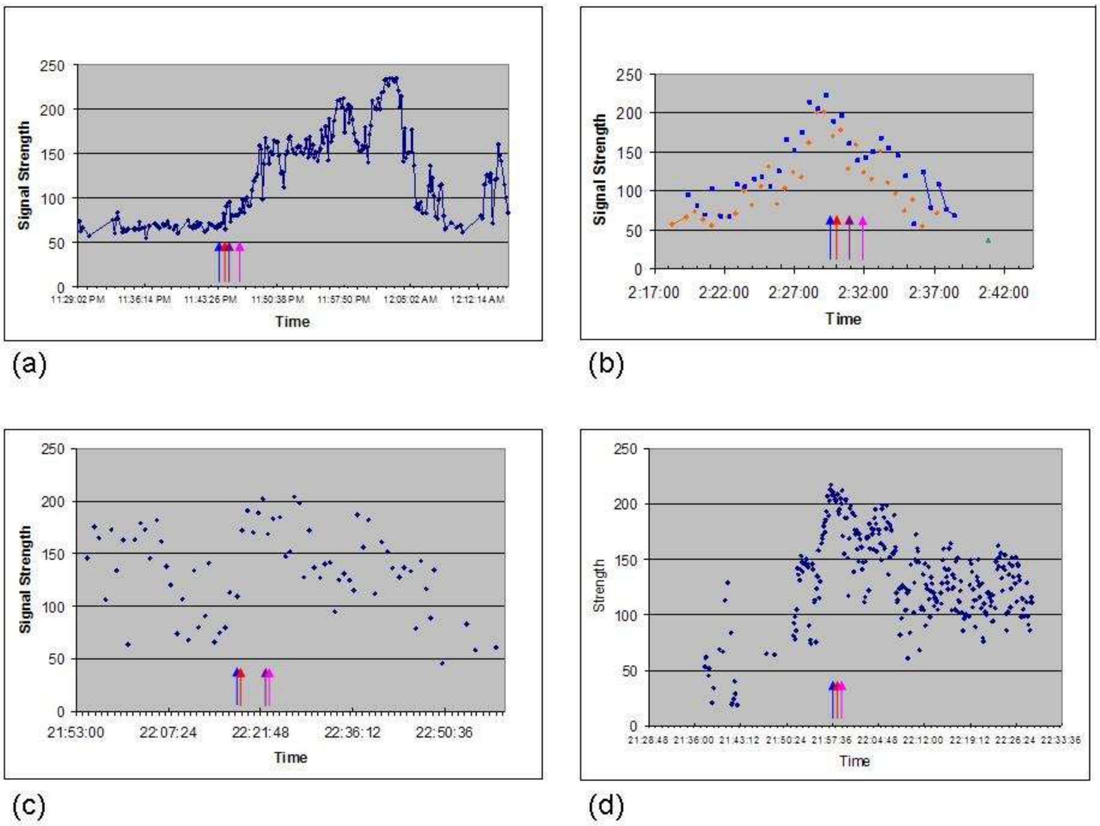


Figure 4.5. Group yip-howl responses to playback, indicating the target animal's radio-collar signal strength (blue points) during the experimental period and the timing of vocal responses. Trials shown are with coyotes: (a) CH683; (b) CH301 (PACK members' signal strength indicated by orange and green points); (c) OH582; and (d) OH742. Data represented in graphs (a), (b), and (c) were collected during the PAIR playback condition, while the data in graph (d) were collected during the PACK playback condition. Blue and red arrows indicate playback start and end times, respectively. Purple and pink arrows indicate vocal response start and end times, respectively.

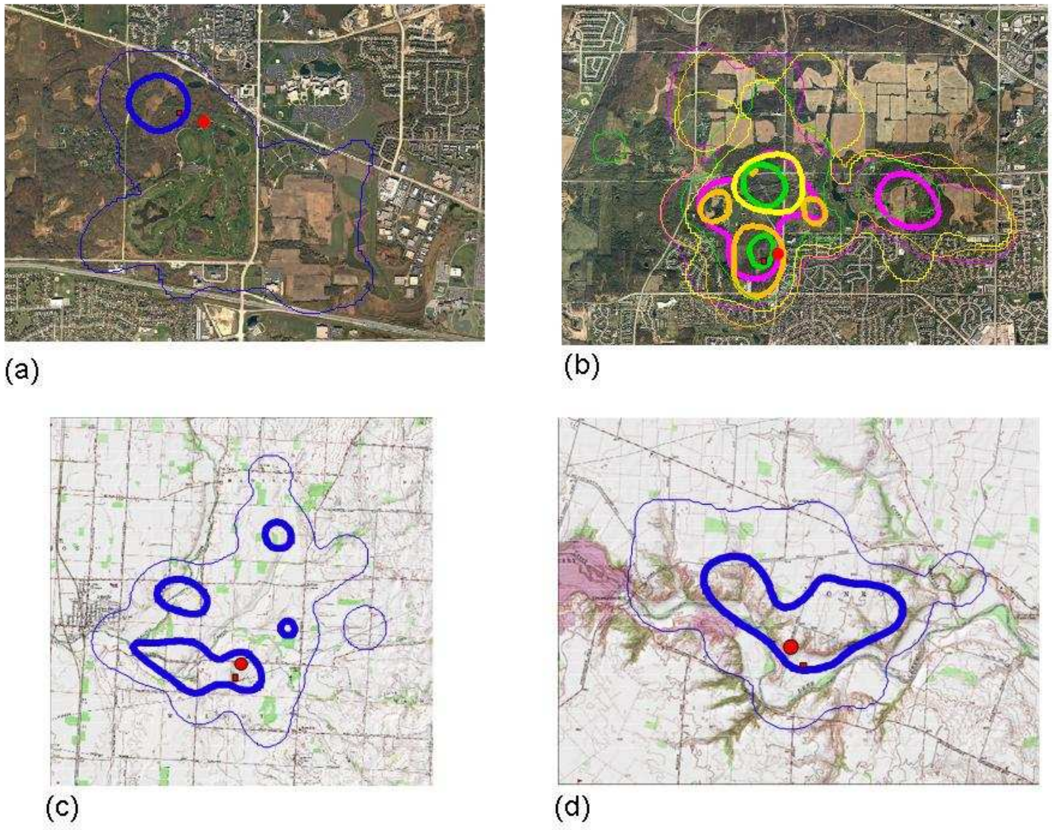
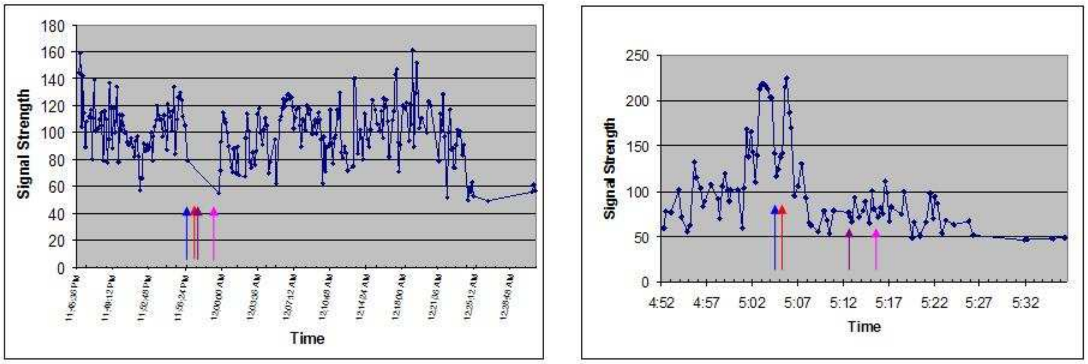


Figure 4.6. Digital maps indicating the location of the playback apparatus (red circle) and the target animal's location (smaller red square) during playback trials in which group yip-howls were recorded. The target animal's 95% UD home range is outlined with a light-weight blue line, and its 50% UD core territory is outlined with a heavy-weight blue line. Trials shown are with coyotes: (a) CH683; (b) CH301; (c) OH582; and (d) OH742. Data represented in graphs (a), (b), and (c) were collected during the PAIR playback condition, while the data in graph (d) were collected during the PACK playback condition. Note that home range and core territory contours are not shown in map (b) for target animal CH301, since too few locations were available for this animal to estimate these UDs. However, the UDs of CH301's family group are shown (pink = alpha female; orange = alpha male; green and yellow = siblings).

Barking and bark-howling were recorded during two playback trials. One of these responses, to a PAIR-condition stimulus, occurred within the 5-minute post-trial period; the other, following a PACK-condition stimulus, occurred almost eight minutes after the end of the playback stimulus presentation. The response to the PAIR stimulus started 19 seconds after the playback stimulus ended. Only one coyote in relatively close proximity to the playback apparatus was heard in both cases.



(a) (b)

Figure 4.7. Barking/bark-howling responses to playback, indicating the target animal's radio-collar signal strength during the experimental period and the timing of vocal responses. Trials shown are with coyotes: (a) OH502 and (b) CH223. Data represented in graph (a) were collected during the PAIR playback condition, while the data in graph (b) were collected during the PACK playback condition. Blue and red arrows indicate playback start and end times, respectively. Purple and pink arrows indicate vocal response start and end times, respectively.

As in the trials during which group yip-howl choruses were recorded, the target animals in both of these trials were located within their core (50% UD) territories at the time of setup (Figure 4.8).

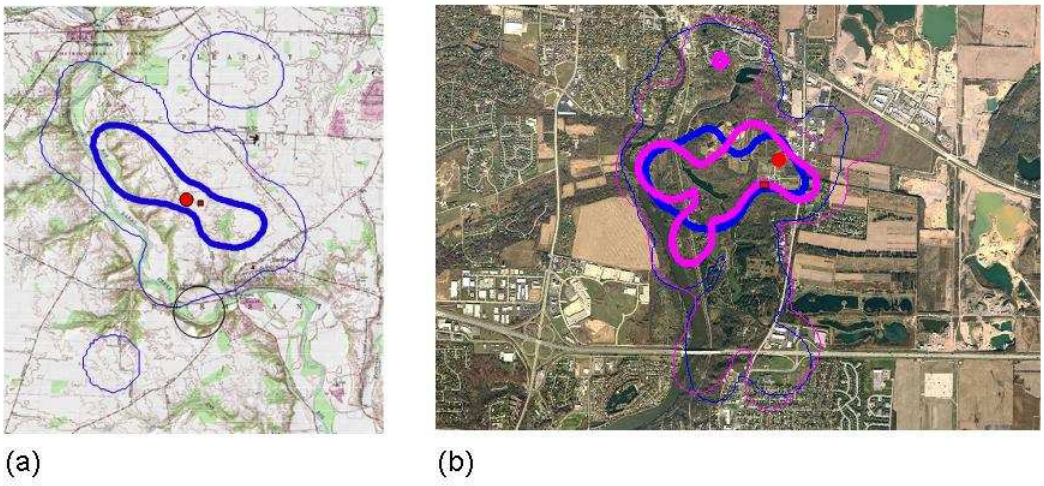


Figure 4.8. Digital maps indicating the location of the playback apparatus (red circle) and the target animal's location (smaller red square) during playback trials in which barking/bark-howling was recorded. The target animal's 95% UD home range is outlined with a light-weight blue line, and its 50% UD core territory is outlined with a heavy-weight blue line. Trials shown are with coyotes: (a) OH502 and (b) CH223. Data represented in graph (a) were collected during the PAIR playback condition, while the data in graph (b) were collected during the PACK playback condition. Note that home range and core territory contours (pink) are also shown in map (b) for a female coyote (CH353), potentially CH223's mate.

Discussion

The results of the study presented here, indicating that coyotes were more likely to approach PAIR playback stimuli and move away from PACK playback stimuli, support the hypothesis that coyotes can judge the relative number of individuals present from the sound of a group yip-howling chorus. We predicted that animals would approach the source of a small-group howling bout more frequently than they would approach a howling bout produced by a large group of coyotes, as this behavior would be consistent with game-theoretical models of agonistic behavior. The odds of a resident individual or small group winning in a direct conflict would be greater against a pair of intruders than against a group of five (as represented by the PACK playback stimulus).

Given that coyotes are typically solitary hunters and often move about their range alone, the occasions in which residents were with several group members at the time of the playback trials were probably few. In addition, the coyote groups in the recordings used as playback stimuli were unfamiliar to the radio-collared coyotes that served as target subjects in the present study. Resident coyotes would be expected to be familiar with the vocalizations of coyotes in neighboring groups (Bradbury & Vehrencamp, 1998), but unfamiliar voices of strangers would likely be considered intruders. Upon hearing a group yip-howl produced by a pair of stranger coyotes, it would be expected that a resident animal, especially the alpha male or female, would approach to investigate, if not to drive the intruders from the vicinity. Gese (2001) reported that resident coyotes, particularly alpha males, would drive intruders from their territory even when outnumbered by one or two. However, resident coyotes hearing a howling chorus produced by five strangers would not be expected to confront the intruders unless they were in a social group approximately equal in size to the intruding pack.

Analyses of coyotes’ responses with respect to their location in the home range and whether they were alone or with others during the PACK playback trials, indicated that the target animals most often moved away from the PACK stimulus, regardless of whether they were inside or outside their core territory or whether they were alone or with other group members. These results are not surprising. As discussed above, the probability of a target animal having been in the presence of four of its pack members during the playback trial was low. In addition, packs of five or more coyotes are not believed to be common in human-populated areas (Roy & Dorrance, 1985). If the resident-to-intruder (i.e., target-to-playback) ratio was low, agonistic theory would predict that the resident(s) would avoid direct conflict. This prediction has been tested with other group-living species. Lions (McComb et al., 1994), male black howler monkeys (Kitchen, 2004), and chimpanzees (Wilson et al., 2001) have been found to approach playbacks of territorial vocalizations when the numeric odds favor the resident group.

The analyses of responses to PAIR playbacks with respect to the territory and social configuration variables, although non-significant, indicated that a resident coyote might be more likely to approach a pair of intruders when either the intrusion occurs within the resident's core territory or when the resident is with other group members. These responses would agree with those predicted by models of agonistic behavior. A resident coyote, already in possession of a territory and its resources, would be the likely winner in a direct conflict against an intruder. In actual observations of coyote conflict, Gese (2001) found that residents consistently succeeded in driving intruders from their territories, even when outnumbered by one or two. This suggests that even a single resident would approach an invading pair when within its territory boundaries. Such energy expenditure might be unnecessarily costly outside the integral core area of a resident's home range. However, resident coyotes may have decided to approach the PAIR playback when with at least one other group member to investigate any potential new rivals in the vicinity.

A long-distance, broadcast announcement of territory ownership allows competing groups to avoid direct confrontation, which expends a great deal of energy and can result in life-threatening injuries. However, the decision to vocalize is also risky, in that the vocalizing animal will be giving away its current position and potentially inviting attack (Harrington & Mech, 1979). Therefore, territorial vocalizations would be expected to occur most frequently in locations of greatest resource importance to the animal. Harrington and Mech (1979) found that they were able to elicit significantly higher rates of howling response from wolves when the animals were at rendezvous or kill sites than when they were in other locations throughout their range.

The findings presented here further support the idea that group yip-howling choruses serve as territorial signals. Each of the four GYH responses occurred when the target animal was within its core territory. In addition, responses were elicited when the target animal was with other members of its social group, a fact implied by the “group” aspect of the vocalization. The Ohio trials cannot be interpreted with respect to target animal’s status of alone or with others during the playback trials, as only one member of a social group was collared in that population. However, more information was available in the Illinois trials since typically at least one other group member, and often both alpha animals in a group, were radio-collared. Although we cannot be certain that the target animals were alone during trials in which their radio-collar beacons were the only signals registering on the datalogging receiver, there were two trials in which the target animal was in its territory and no other radio-collar signal was detected. In six additional trials the target animals were known to be with other group members, but were located outside their core territory. No vocal responses to the playback stimuli occurred in any of these trials.

Although coyotes have been described as the most vocal mammal in North America, vocal responses were elicited in only 16% of the playback trials conducted in this study. Fulmer (1990) and Mitchell (2004) also reported more approach movements than vocal responses by coyotes in response to playbacks. However, Gese (2001) reported that vocal bouts were more likely to follow than precede direct conflicts between groups. Vocal response rates in this study were similar to those found by Mitchell (2004), but were substantially lower than the 41% response rate found by Fulmer (1990).

The movements and vocal responses of the coyote groups tested in these playback trials were consistent with those of other group-living species when challenged by potential intruders (Kitchen, 2004; McComb et al., 1994; Seddon & Tobias, 2003; Wilson et al., 2001). Although the number of animals in the coyote groups in this study was not known, precluding precise analyses of resident-intruder ratios, our results suggest that coyotes glean information about group size from group yip-howl choruses and use this information in decisions regarding confrontation with competing groups.

CHAPTER 5

SUMMARY AND SYNTHESIS

The studies presented in this dissertation investigated whether cues to group size might be present in the group yip-howl chorus of the coyote (*Canis latrans*). Acoustic features of the primary vocalizations that comprise the chorus (howls and barks) were analyzed to determine whether individual voices were distinguishable. Experiments with human subjects were conducted to examine the potential of particular perceptual cues to provide group-size information, and field playback experiments measured the responses of radio-collared coyotes to choruses produced by different-sized groups. In addition, home-range contours of the radio-collared coyotes were calculated to assist in determining playback site locations and interpreting results of playback experiments.

Overall Summary of Results

Nineteen coyotes (9 male; 10 female) were radio-collared in central Ohio from December 2003 to March 2006 (Chapter 2). These animals were tracked using radio telemetry from the date of collaring to the time of the animal's death or the end of the study period in October 2006. Home-range contours were calculated from the telemetry data to determine the sizes of the coyotes' overall home ranges (95% utilization distribution, UD) and core territory (50% UD). Five small-range resident animals were found to traverse annual 95% UDs that ranged in size from 3.1 to 24.7 km^2 and to hold core territories ranging from 0.9 to 3.5 km^2. Other coyotes were described as wide-ranging residents (2 coyotes), transients (2), dispersers (2), and settlers (3). Three animals were killed and two were lost before sufficient location data could be collected. Mortality data indicated that all animal deaths in the study were a result of human actions. Thirteen of the nineteen animals (68.4%) died, resulting in an overall long-term survival probability of 0.04 over the 37 months of the study.

Coyote group yip-howl choruses were recorded at eight zoological facilities in the United States (Chapter 3). The captive groups ranged in size from two to five coyotes and were comprised of different combinations of male and female animals. Features of the overall chorus, such as duration and entry of voices, and acoustic features of the howl and bark vocalizations produced during these bouts were analyzed from video and audio recordings to determine whether voices of individual animals could be distinguished. The features of primary interest in the howl and bark vocalizations were: duration; fundamental frequency at the beginning, middle, and end points; frequencies and relative amplitudes of harmonics; spectral contour; and harmonic-to-noise ratio. Comparisons of chorus length and group size revealed no relationship between these two variables, indicating that group size does not appear to affect the length of chorus howls. Analyses of the timing of entry into the chorus and individual howl duration revealed that coyotes typically overlap when producing howls during the introductory portion of the chorus. Cross-validated discriminant function analyses to determine individual voice differences performed on howl vocalizations within each of the groups resulted in an average overall correct classification of 73%, whereas classification of barks averaged 63.5%.

To better understand how coyotes might perceive howling choruses and “hear out” the number of vocalizing individuals, human subjects were recruited to serve as “substitute” perceptual systems and asked to estimate coyote group size from segments of group yip-howl choruses presented to them (Chapter 3). Subjects listened to segments taken from the introductory, howling portion of the chorus and from the latter, yipping portion. Although the overall percentage of subjects able to precisely guess the number of coyotes vocalizing in the chorus was low (32% for the introductory portion and 27% for the yipping portion), all mean estimates of group size were within 1.0 of the actual group size for the howl segments and within 1.7 for the yipping segments. Acoustic features related to individual voice characteristics and different or same vocalizations occurring simultaneously or in an alternating fashion were given as the most important cues indicating group size in both the howl and yipping portions of the chorus. However, striking differences were found in the use of other cues between the two chorus sections. Timing cues, related to the entry of voices and the onset and offset of individual vocalizations, were described as important features used to estimate group size in over 25% of the subjects’ comments for the howl segments, but in less than 5% for the yip segments. Conversely, rhythm cues, related to the cadence of the vocalizations, were described as important features in almost 16% of subjects’ comments for the yipping segments, but were never discussed in relation to the howling segments.

A field playback experiment was conducted with nineteen radio-collared coyote populations in central Ohio and northeastern Illinois (Chapter 4). The experiment consisted of two playback conditions: a PAIR condition, in which a recording of a male-female pair of coyotes was used as the playback stimulus; and a PACK condition, in which a recording of a mixed-sex group of five coyotes was the playback stimulus. Each target animal was presented with both conditions separated in time by at least 1.4 days. A datalogging receiver and a microphone and tape recorder at the location of the playback speaker recorded the target animal's movement towards or away from the stimulus and any vocal response produced by the target animal, respectively. Movement was measured using the transmitter signal strength as recorded by the datalogging receiver, with higher signal strength indicating movement toward the stimulus, and lower signal strength indicating movement away from the stimulus. The results of this experiment indicated that target animals tended to move away from the PACK stimuli and approach the PAIR stimuli. The four group yip-howl responses to the playback stimuli were all elicited during trials conducted when the animals were within their 50% UD core territories.

Ohio Radio-Tagging Study of Coyotes

The home range and territory sizes of coyotes in this study were similar to those observed in other studies of coyotes in similar landscapes. Many factors are assumed to contribute to the size of these home ranges, including food abundance and the availability of areas offering protective cover and sites suitable for denning. Coyote home ranges are believed to decrease in size with an increase in habitat fragmentation due to human activity. Therefore, although coyotes in unexploited areas may traverse relatively large ranges, coyotes in more densely human-populated areas maintain smaller territories. It seems there is a threshold of resources below which coyotes cannot survive. Although this threshold has not yet been determined, it is obvious that even within regions with extensive human development and activity, coyotes can carve out an area that fulfills their resource requirements for survival and reproduction. Unfortunately, the sample size in the present study was not sufficient to make meaningful comparisons between animals living in different habitat types.

The high mortality observed in the Ohio population was surprising. Even though coyotes are considered a nuisance species by the State and there is no closed hunting season in effect, it was not expected that such a high number of study subjects would be killed during the study period. Of course these mortality rates cannot be extrapolated to all regions of Ohio. The primary study sites were within regions with a long history of farming, which remain largely agricultural today. Human perceptions of coyotes as vermin in these farming regions are common and many residents participate in seasonal hunting and trapping activities. These phenomena could skew the results toward a higher mortality rate than might be found in suburban areas or regions comprised of extensive park, or even industrial, lands.

A tangential finding of this research was that there is a tremendous need for public education regarding the coyote’s ecology and behavior. Although people in suburban areas generally appear to hold more compassionate views toward the coyote’s relatively recent increase in population density, it seems that attitude might not be upheld once residents become aware of coyotes living in their own backyards – sometimes quite literally. When this occurs, health and safety concerns are raised, similar to those commonly voiced in agricultural communities. Public education could serve to mitigate these fears and potential escalation of human-coyote conflict.

Group Size Cues in the Group Yip-Howl

Taken together, the results of these studies support the hypotheses that 1) the coyote group yip-howl chorus contains group size cues, and 2) coyotes use this information in deciding whether to approach potential rivals. In addition, these results serve to further affirm the role of the group yip-howl chorus as a territorial signal.

As described in Chapter 1, a number of studies conducted over the past 15 years have investigated whether the assessment strategy modeled to describe decision-making in conflict escalation between individuals is applicable to agonistic encounters between competing groups. The results of those studies indicated that information about group size might be available in species-specific group territorial vocalizations, and that conspecifics hearing those vocalizations adjust their behavior in a manner consistent with that predicted by game-theoretical models of competitor assessment in agonistic encounters. Specifically, territorial groups tend to approach playbacks of group vocalizations produced by groups smaller than their own, but do not approach, or retreat from, groups larger than their own. The results of the field playback experiment conducted in the present study showed a similar response pattern, with target animals retreating from the PACK playback and tending to approach the PAIR playback.

Studies of black howler monkeys and chimpanzees focused on the responses of males only. McComb et al.'s (1994) study of lions focused on the response of female lions but also addressed differences between female and male responses. Unfortunately, the sample size and lack of specific information about group composition during playback trials in the present study precluded such analyses, but differences in group configurations might have especially affected responses to PAIR stimuli. Female lions were more cautious and less likely to approach than males, who typically approached unless they were outnumbered by one to three animals. It is possible that coyotes respond in a manner more similar to female lions or that a difference between male and female responses existed but was not demonstrated in the present study. Some support for the latter is offered by Gese (2001), who reported that alpha male coyotes were often observed successfully driving intruders from their territory even when outnumbered by one or two. Alpha females were not as likely to respond as aggressively. In addition, it was suggested that both lions and chimpanzees might cautiously respond to vocalizations by one or two animals until they are satisfied that the vocalizing animals are not accompanied by other silent intruders.

None of the group-assessment studies of other species reported whether all group members were known to participate in group territorial vocalizations. Interestingly, this lack of participation by some members of the group would represent a dishonest signal that is not a bluff. Instead, it would seem like a "set-up." This would be unexpected if the signal were solely meant to advertise RHP. However, it is possible that some of these vocalizations are initially produced for other purposes, based on different motivations than territorial defense.

Personal observations of coyotes and wolves in captivity revealed that the animals were in an aroused state when howling and howling was more likely to be elicited from a group that was physically active than one that was inactive. Perhaps this illustrates the signal's role in group cohesion, while simultaneously serving to advertise territorial ownership and the territory owner's presence. It could be that spontaneous choruses do not necessarily involve all group members, but perhaps groups respond vocally to other groups' choruses only if the group size ratio is in their favor. Possibly, the group yip-howl of a competing group could lead to increased arousal and congregation in nearby groups, who then vocally respond if enough group members are present to even the odds. McComb et al. (1994) suggested that some roaring by female lions in response to playback served to recruit absent pride members.

Additional studies utilizing interactive playback could help to distinguish between contexts in which group yip-howling might serve different functions. Perhaps spontaneous howling choruses differ from those produced in response to a competing group's chorus, as Radford (2003) reported for the territorial vocal rallying of the green woodhoopoe. The woodhoopoes were found to produce longer rallying choruses in response to playbacks of larger groups, thereby potentially inflating the defending group's perceived size. Seddon & Tobias (2003) also found that subdesert mesite groups retreated from large-group chorus playbacks, but when they did vocally respond the responses involved more group members and were sustained for a significantly greater duration than those produced in response to the solo songs of potential male intruders.

Previous studies investigating potential numerical assessment of competing groups to determine rivals' RHP also employed playback techniques to investigate whether information about group size might be available in territorial group vocalizations and used by conspecific groups in assessing RHP of competitors. However, the present study is the first to concurrently analyze acoustic features of the group vocal signal in this context. Analysis of the acoustic signal can elucidate the specific features of the vocalization that might allow for accurate numerical assessment, allowing for the formulation of hypotheses that could be tested through different experimental conditions that vary these features in the playback stimuli.

From a practical perspective, analysis of the group vocalization could lead to understanding of signal features that might assist wildlife biologists in development of acoustic censusing techniques. For elusive, difficult-to-study species such as the coyote, such a technique could greatly assist in ascertaining much-needed population density estimates. For example, vocal bouts might be elicited through playback of conspecific vocalizations or sirens and recorded. Recordings gathered in the field could be examined further to determine the number of animals vocalizing. Further research could possibly lead to an even better understanding of patterns in the vocal signal that could lead to techniques for counting group numbers in the field, and perhaps even identifying individuals or the sexes of the animals participating in the chorus.

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