

Coyote Vocal Communication and Its Application to the  
Selective Management of Problem Individuals

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## Abstract

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University of California, Berkeley

Professor Reginald H. Barrett, Chair

Livestock depredation by coyotes severely affects ranchers, and the existing evidence implicates breeding coyotes in the majority of livestock losses. Management approaches that target these problem individuals will be the most effective way to reduce livestock losses. This dissertation examines coyote long-range vocal communication and the likely usefulness of recorded vocalizations for selective coyote control.

The information content of barks and howls is important because coyotes may recognize vocalizing individuals. This could cause coyotes to respond differently to playbacks depending on the individuals used. It is also important to understand how vocal characteristics change over biologically relevant distances, since these changes provide insights into the practical communicative significance of long-range vocalizations. I investigated whether coyote barks and howls were individually distinctive using 293 barks and 280 howls from 7 coyotes. Barks and howls were individually specific: discriminant analysis correctly classified the barks of 5 coyotes 69% of the time, and the howls of 6 coyotes 79% of the time. Howl characteristics did

not degrade with distance, and discriminant analysis was 75% accurate at assigning howls recorded at multiple distances to 6 individuals. Bark characteristics were unstable with distance and it is unlikely that barks could be used for individual recognition. Howls and barks probably serve separate functions: howls are optimized to convey information, while barks are suitable for attracting attention and for facilitating distance estimation. Effective playbacks should incorporate both types of vocalization so that the complementary information they contain is available to listeners.

A year-long experiment investigated the selectivity and efficacy of a variety of acoustic stimuli for calling coyotes. Transients rarely responded vocally, and territorial coyotes commonly responded to group coyote vocalizations. During optimal conditions, vocal response rates were over 55% for territorial males, 42% for alpha females, 11% for beta females, and below 4% for transients. Territorial coyotes were more likely to approach playbacks than transients, and coyotes more readily approached group howls than other playback types. When conditions were optimal, approach response rates were 47% for alphas, 49% for betas, and 27% for transients. These results suggest that playbacks can be used for selective coyote control.

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## **CHAPTER 1. COYOTE DEPREDATION MANAGEMENT: CURRENT METHODS AND RESEARCH NEEDS**

**Abstract:** This paper examines the severity of livestock depredation by coyotes, reviews evidence implicating breeding – or alpha – coyotes in the majority of incidents, evaluates currently used depredation control techniques, and suggests directions for future research. Nonlethal control ranges from varied animal husbandry practices to coyote behavioral modification or sterilization. These methods show significant promise but have not been proven effective in controlled experiments. Many livestock producers therefore rely on lethal control, and most of these employ nonselective strategies aimed at local population reduction. Sometimes this approach is effective and other times it is not. This strategy can fail because the alpha coyotes that are most likely to be killing livestock are the most resistant to nonselective removal techniques. An alternative is selective lethal control. Livestock Protection Collars (LPCs) and coyote calling are the primary selective lethal approaches. However, LPCs do not have support from the general public due to the toxicant used, and the factors affecting the selectivity of coyote calling have not been studied. The greatest impediments to effective coyote depredation management are currently: (1) a scarcity of selective control methods; (2) our lack of understanding of the details of coyote behavioral ecology relative to livestock depredation and wild prey abundance; (3) the absence of solid research examining the effectiveness of different control techniques in a variety of habitats and at multiple predation intensities; and (4) the dearth of rigorous controlled experiments analyzing the operational efficacy of selective removal versus population reduction.

**Key words:** *Canis latrans*, coyote, depredation, livestock, nonlethal control, population reduction, selective control, sheep.

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## **COYOTE DEPREDAATION ON LIVESTOCK**

Coyotes are vilified throughout the western United States as insatiable livestock killers. This impression is based on the fact that coyotes are the most important predator of sheep, goats, and cattle. Sheep producers attributed 39,800 sheep and 126,000 lamb deaths (valued at \$9.6 million) to coyotes in 1999; this was 61% of the losses they ascribed to predators, and 22% of their total losses (National Agricultural Statistics Service 2000c). Coyotes therefore ate their way through 2.3% of the country's 1999 sheep population, which was estimated at 7.2 million individuals (National Agricultural Statistics Service 2000b). Coyotes were blamed for the deaths of 21,700 goats in Arizona, New Mexico, and Texas in 1999, out of a total population of 1.3 million. This accounted for 35.6% of the total loss to predators, at an economic cost of \$1.6 million (National Agricultural Statistics Service 2000b, c). Predation was a minor cause of loss to the cattle industry; coyotes killed less than 0.1% of the United States' total cattle population in 2000 (National Agricultural Statistics Service 2000a, 2001). In 1995 only 2.7% of total cattle losses were due to predation (and 1.6% of the total cattle losses were due to coyotes). Respiratory problems, digestive problems, calving problems, and weather each killed 6 to 17 times more cattle than coyotes did (National Agricultural Statistics Service 1996). Nevertheless, coyotes were the dominant cattle predator; they were implicated in 65% of cattle losses due to predation in 2000, or 8,000 cattle and 87,000 calves worth a total of \$31.8 million (National Agricultural Statistics Service 2001).



Based on these statistics, coyotes are responsible for over \$40 million in damages to livestock producers every year, with proportionally more damage to sheep and goats than to cattle. While this may seem negligible in the face of the \$638 million value of the United States sheep industry in 1999, and the \$67 billion value of the United States cattle industry in 2000 (National Agricultural Statistics Service 2003), the livestock industry traditionally operates on slim profit margins. For example, a survey with 76 respondents (representing approximately 5% of United States lamb meat production) revealed that net profits per ewe were \$3.70 in 1997, -\$3.95 in 1998, and -\$4.06 in 1999. During this period the annual proportion of ranchers that lost money ranged from 36% to 64% (United States International Trade Commission 2002). Losses of livestock due to coyote predation can easily transform a narrowly profitable operation into an unprofitable one. The problem is compounded by the fact that coyote damage is not spread equally among producers. High losses at a Montana ranch were documented by O’Gara et al. (1983). These researchers reported 24% and 27% of lambs lost to coyotes during a consecutive 2 year period with minimal coyote control, and a 13% loss in the third year despite intensive control. In general, large sheep operations tend to be harder hit by depredation, with 10% of all sheep producers typically losing more than 20% of their lambs to coyotes (Wagner 1988:29-36). Producers generally choose to protect their economic interests by controlling their losses, including those related to predation. Because coyote control is so prevalent in ranching areas, it is worth examining the available data concerning coyotes that kill livestock, and then evaluating depredation management strategies in light of this information.

## **NOT ALL COYOTES KILL SHEEP**

Many people believe that every coyote will kill sheep if given the chance. For example, Timm and Connolly (2001) blamed elevated levels of depredation on increased predator abundance at the University of California's Hopland Research and Extension Center (HREC). There is some evidence that supports a relationship between coyote population size and depredation levels, particularly when wild prey is unavailable. Pearson and Caroline (1981) observed that livestock predation rates were highest during periods of low rainfall, when prey populations were presumably at low levels; and O'Gara et al. (1983) noted that predation was highest when sheep arrived on their summer range, which coincided with low rodent populations and coyote pup weaning. A non-significant trend between coyote abundance indices and sheep losses was found by Robel et al. (1981).

Stoddart et al. (2001) analyzed 6 years of data during a jackrabbit irruption and decline at an Idaho site. They concluded that predation rates on ewes and lambs were proportional to coyote density, and that coyote population reduction would therefore alleviate sheep losses. However, this relationship was not convincingly demonstrated. For example, total losses were used as a proxy for losses due to coyotes, under the assumption that non-predation mortality factors were constant during the study. Meanwhile, other lines of evidence strongly indicate that only certain coyotes kill sheep. Connolly et al. (1976) studied the sheep-killing behavior of captive coyotes at HREC, and reported that older males and the females they were paired with were highly likely to attack and kill sheep, while younger males rarely attacked sheep and unpaired females never killed sheep. When mated pairs attacked sheep, the male almost always took the

lead. A subsequent series of field studies at HREC (Conner et al. 1998, Sacks et al. 1999b, Blejwas et al. 2002) found that breeding (or “alpha”) coyotes whose territories overlapped sheep were the primary livestock depredators, and that nonbreeders were rarely associated with sheep kills.

Till and Knowlton (1983) found that killing the pups of depredating alpha coyotes (denning) reduced sheep kills by 88% in the week following removal, and that killing pups and the breeding pair reduced sheep kills by 98%. These researchers suggested that the need to provision pups caused breeding coyotes to maximize foraging efficiency by focusing on large and easily killed prey. They raised the possibility that sterilized coyotes might abstain from killing while maintaining exclusive territories that prevent intrusion by other coyotes. One study has shown a reduction in sheep depredation by sterilized coyotes (Bromley and Gese 2001b). This research was conducted in an area where sheep had not been recently grazed, and each pack was exposed to sheep for only 5 to 23 days per year. While it is promising that the surgically sterilized packs maintained their social structure for the 3-year study (Bromley and Gese 2001a), it remains to be seen if sterilized coyotes will avoid killing sheep that are available for longer periods.

The evidence from HREC suggests that dominant, pair-bonded coyotes will eventually kill sheep if they are available within the coyotes’ territory year-round (Blejwas et al. 2002). At HREC, lambing occurred in the winter – before pups were present – yet the dominant coyotes still killed lambs (Sacks et al. 1999b). The authors of this study suggested that paired coyotes work cooperatively to attack larger ungulate prey that they would not be able to handle alone. These coyotes may start off with smaller lambs in the winter, and then work their way up to adults as they gain experience.

Alternatively, the pressures of provisioning pups in the spring may cause alpha coyotes to initially attack older lambs and then adult sheep. Experience with older sheep may then lead to a higher likelihood of coyotes attacking young lambs when they become available the following winter. Observations of coyote attacks on wild ungulates (Gese and Grothe 1995) support the notion that the breeding pair (and particularly the male) takes the lead in successful ungulate attacks, and that coyotes do cooperate when making kills. It is reasonable to assume that attacks on other ungulates, such as sheep, goats, and calves, would be conducted in a similar manner.

The available evidence indicts breeders for the vast majority of coyote-caused livestock losses. This evidence does not preclude the possibility of an effect of coyote density on depredation levels, because the number of breeders or their behavior relative to sheep may vary with coyote population density and wild prey abundance. For example, regions with high coyote density are typically better coyote habitat, with smaller territory sizes and more breeders per unit area. Increases in depredation levels as wild prey populations decline could be primarily due to an increase in livestock kills by breeders (as opposed to the coyote population as a whole).

Eradicating all coyotes in an area would certainly stop coyote depredations, but this approach may not be cost-effective and has potential ecosystem-level repercussions, such as mesopredator release (Crooks and Soulé 1999) and increased rodent populations (Henke and Bryant 1999). Control methods will be most effective and ecologically sound when they remove the threat posed by breeding coyotes that live where livestock are pastured. The best depredation management techniques would be selective towards specific problem animals, effective at reducing livestock losses for an extended period,

have minimal environmental impact, be socially acceptable to the general public, and cost less than the losses they prevent.

## **NONLETHAL DEPREDAATION MANAGEMENT**

A number of animal husbandry techniques show promise for meeting these criteria. Fences can be built that, when properly maintained, are nearly 100% effective at preventing coyotes from accessing livestock (deCalesta and Cropsey 1978, Conover 2002:300-301). Birthing in sheds, keeping herders with livestock during the day, bedding animals for the night near people, removing or burying carcasses, and lighting corrals where stock are kept at night have all been suggested to reduce depredation (Davenport et al. 1973, Nass 1977, Tigner and Larson 1977, Conover 2002:325-326). Guard animals may also effectively protect livestock, though not in all circumstances. Guard dogs are commonly used by Europeans and native Americans, and the majority of people who employ dogs to protect sheep and goats say that they reduce predation (Black and Green 1984, Green et al. 1984). Donkeys and llamas, which have a natural dislike for canids, have also been successfully used as guard animals (Conover 2002:240).

These husbandry techniques are all selective, in that they aim to prevent coyotes that are intent on killing livestock from contacting their prey, and they all seem to be effective in certain situations. The public generally approves of these methods because they are nonlethal, selective, and do not cause serious ecological damage. However, some do have ecological impacts; for example fencing may inhibit wildlife movements (Knowlton et al. 1999), range quality decreases in and around confined bedding grounds (Davenport et al. 1973, Wagner 1988), and guard dogs will occasionally harass wildlife (Black and Green 1984). These husbandry practices also have significant up-front and

maintenance costs that must be borne by the producer, ranging from material costs for fencing and sheds to labor costs for herding livestock and training dogs. Guard dogs carry an additional risk, since up to 10% of them eventually harass or kill livestock (Green et al. 1984).

An alternative class of nonlethal depredation management techniques – behavioral modification – has received considerable attention. The aversive conditioning (or “Clockwork Orange”) approach involves using negative reinforcement to train individual coyotes to avoid killing livestock. One experiment with captive coyotes successfully trained 3 of 4 individuals to avoid rabbits (Olsen and Lehner 1978). Another experiment found that coyotes fitted with electronic shock collars could be trained to avoid sheep (Andelt et al. 1999). Both of these studies documented behavioral changes that lasted for over 4 months. However, the expenses involved in capturing and conditioning all coyotes in an area that could potentially depredate livestock undoubtedly exceeds the benefits in the majority of situations. Recent research at the National Wildlife Research Center (Shivik and Martin 2000) could make aversive conditioning more cost-effective by using sound-activated shock collars that are attached to coyotes when they pass through snares; the collar would be activated by special bells attached to livestock. Coyotes that chased animals wearing the bells would be shocked until they left the vicinity.

Another aversive conditioning approach involves using an emetic (such as lithium chloride) in sheep carcasses and baits to train coyotes to avoid live sheep. There is, however, no evidence that coyotes actually generalize from the baits to live sheep, and

producers who tried this technique invariably stopped using it because they felt it was not worthwhile (Conover and Kessler 1994).

Other behavioral modification strategies try to frighten or repel coyotes away from their prey without relying on a conditioning or training phase. Lehner et al. (1976) tested over 45 potential olfactory repellents and did not find any that produced an avoidance reaction. They concluded that olfactory repellents were only likely to work in combination with actual aversive conditioning. Other researchers have used light or sound to scare coyotes. Linhart spent several years developing an “electronic guard” incorporating a strobe light and alarm (Linhart et al. 1984, Linhart et al. 1992). He felt that these devices were effective for extended periods when multiple guards were used. However, the first experiment was uncontrolled and had several trials (4 of 15) where predation ceased for less than 4 weeks, and the second experiment was biased in its presentation of loss reductions. Linhart compared total losses during the entire summer (10 to 12 weeks) for the year before experimental trials with losses during the latter portion of the summer (less than 8 to 10 weeks) that guards were used. This bias would be enhanced if losses decreased through the summer as lambs got larger and breeding coyotes stopped provisioning pups (O’Gara et al. 1983).

Fright tactics like the electronic guard are vulnerable to habituation of coyotes to the stimuli used. The devices may not be effective for more than a few days, and they are usually not recommended for reducing livestock depredation (Koehler et al. 1990, Conover 2002:232-234). These techniques might work better if guard device activation was contingent on predator behavior instead of random. When a device fires randomly, coyotes may learn that activation has nothing to do with them. If the device only

activates when the coyote approaches a particular pasture or engages in a certain behavior, the coyote is more likely to associate activation of the device with its own actions (Shivik and Martin 2000). Field tests of a Radio Activated Guard (RAG) that was triggered by wolf radio transmitters had promising results (Breck et al. 2002), and controlled trials with coyotes showed less habituation to behavior contingent alarms than to randomly fired alarms (Shivik and Martin 2000). Behavior contingent frightening stimuli may become an attractive control option, particularly if the prohibitively priced (\$3,800) RAG could be made affordable by using inexpensive motion or infrared sensors that would detect uncollared predators.

Another nonlethal technique is the sterilization of alpha coyotes whose territories overlap sheep. This may reduce depredation when sheep are only seasonally grazed within coyote territories (Bromley and Gese 2001b). However, reproductive inhibition will not eliminate killing if ungulate predation results from pair bonding and cooperative foraging rather than the need to provision pups (Sacks et al. 1999b). There are currently no chemical sterilants available that are proven safe and effective for coyotes and that will not interfere with territorial behavior, and there is no reliable way to distinguish alphas from betas and transients at the time of capture. Therefore, any reproductive inhibition program would require the capture and physical sterilization of all adult coyotes in an area.

## **LETHAL COYOTE CONTROL: POPULATION REDUCTION**

Because all of the aforementioned nonlethal coyote control techniques require significant time and initial expense on the part of livestock producers, lethal control is much more common. This is particularly true when large numbers of sheep are grazed



over an extended area with rough terrain and cover that favors coyotes; non-lethal methods are often impractical under these conditions. Lethal control is also less expensive and less labor intensive for many producers, since they can supplement their own efforts by calling in predator control specialists who are paid through government sources. However, lethal techniques can vary in their efficacy against problem coyotes and in their tendency to affect nontarget species. Leghold traps, snares, and cyanide ejectors (M-44s) can be used in ways that are highly species-selective, by taking care to use appropriate baits, equipment, and techniques. These methods are not always effective at removing problem coyotes, though. Research at HREC in north-coastal California (Sacks et al. 1999a) found that young coyotes were particularly vulnerable to M-44s, and that older and alpha coyotes were rarely trapped or snared during the winter lambing season when depredation losses peaked.

Aerial gunning of coyotes is highly species-selective, since shooters verify the target's identity before pulling the trigger. Aerial gunning is often practiced in a population reduction or "preventative" mode, where coyotes are shot in an area up to 6 months prior to the arrival of sheep. Because preventative aerial gunning is widely touted as an effective management tool, it makes sense to critically evaluate the science that this claim is based on. The best available research on the efficacy of this method (Wagner and Conover 1999) concluded that gunning significantly reduced lamb losses the following summer. This study unfortunately had several problems. Site selection was pseudoreplicated; 6 of the 33 grazing allotments were used 2 or 3 times, which violated the statistical assumption of independent replicates. In addition, the selection of treatment and control plots appeared biased. Wagner and Conover presented data for 22

of the allotments that tested for differences between treatment and control sites. High variability in losses ensured that there were no significant differences in mean losses, yet sites that were later gunned had lower confirmed yearly lamb losses (2.9 versus 5.4), fewer lambs lost to all causes (70 versus 100), and a smaller number of ewes lost to all causes (28 versus 38). The statistical results were also artificially enhanced by a lack of correction for multiple comparisons. Confirmed lamb kills, estimated lamb kills, and lambs lost to all causes were estimated from the same data set, and the alpha level for significance should have been reduced to 0.017. Using the revised alpha level, the only significant result was the finding that gunned allotments had fewer confirmed lamb kills than control allotments. It is unclear whether this result would have been statistically significant if site-selection bias and pseudoreplication were correctly incorporated.

A concurrent study found “no consistent relationship between extent and intensity of aerial hunting and lamb losses or the need for SPM” (Wagner 1997:56), where SPM refers to summer predation management with traps and shooting. Wagner said that the lack of correlation could be explained if gunning effort was biased towards sheep units with more predation, yet there was no correlation between lamb losses for the previous year and the amount or extent of gunning.

Traps, snares, M-44s, and preventative aerial gunning are essentially aimed at reducing coyote population levels; they are nonselective methods used to remove as many coyotes as possible. A study at HREC found no relationship between subsequent lamb losses and the number of coyotes killed using traps, snares, and M-44s (Conner et al. 1998). Wagner (1988:113) said that the population reduction approach is “something of a sledge-hammer one: If enough coyotes are shot, trapped, and exposed to M-44s...

their numbers can be reduced and the chances are that the offending animal(s) will be among those taken and the losses reduced.” While this approach likely works to decrease livestock losses in many cases (e.g. Dorrance and Roy (1976) discuss increased losses in the United States after the 1972 toxicant ban), the general public disapproves of techniques that kill large numbers of innocent animals, and this sentiment contributed to California’s ban on leghold traps and M-44s in 1998 (California Fish and Game Code 1998). In addition, overuse can decrease the efficacy of these techniques (Sacks et al. 1999a) and intensive lethal control affects coyote demographics. Exploited coyote populations have a younger age structure, lower survival, increased juvenile reproduction, larger litters, and smaller packs (Knowlton et al. 1999). If populations are severely reduced, there is also the potential of mesopredator release (Crooks and Soulé 1999), in which small carnivore populations increase and negatively affect birds and small vertebrates. Henke and Bryant (1999) found that when coyote density was reduced by 50%, rodent and rabbit density increased, the abundance of badgers, bobcats, and foxes increased, and rodent species diversity declined.

## **LETHAL SELECTIVE CONTROL**

A few lethal control techniques seem to be selective towards depredating coyotes: livestock protection collars (LPCs) and techniques based on coyote calling. LPCs are the most specific; in one study the devices killed coyotes that attacked sheep in 10 of 14 attacks (Burns et al. 1996). LPCs are rubber collars that can be placed around the necks of sheep or goats; each collar has 2 pouches that are filled with poison. When a coyote attacks the throat of an animal wearing a collar, one or both of the pouches are usually punctured and the attacker ingests the toxicant (Conover 2002:163). Although any

poison could conceivably be used in an LPC, the only chemical currently approved by the EPA is Compound 1080, or sodium monofluoroacetate. Compound 1080 is highly toxic to canids; 5 mg will kill a coyote (Burns et al. 1986).

LPCs filled with Compound 1080 have several drawbacks. The collars are expensive (around \$20 each), the EPA limits the number of collars that can be used in a given area, collars must be closely monitored, and carcasses and spills must be treated as hazardous waste. States are required to have registration, training, and documentation programs before LPCs can be used, and in 1999 only 7 states had these programs in place (Timm and Connolly 2001, Conover 2002:163). In addition, there are risks of accidental poisoning and secondary toxicity from Compound 1080.

Accidental poisoning occurs when non-target animals ingest poison that spills out of a ruptured collar. One milliliter of fluid from an LPC exceeds the LD<sub>50</sub> (the amount of poison that will kill 50% of individuals) of small scavenging birds, golden eagles, all canids, most mustelids, domestic cats, and bobcats (Wagner 1988:126-129). A study examining the potential for non-target poisoning found that domestic dogs were somewhat susceptible to poisoning, and that scavenging magpies tended not to feed on contaminated material (Burns and Connolly 1995). Because coyotes normally feed on the flank, hindquarters, and viscera rather than the neck (Wade and Bowns 1982), coyotes that scavenge another animal's kill are also unlikely to be poisoned. Innocent coyotes are susceptible to poisoning if they eat regurgitant from a poisoned coyote; in one study the researchers believed that a coyote died in this manner (Burns et al. 1986). Secondary toxicity occurs when Compound 1080 levels are high enough in a poisoned animal to affect other animals that scavenge the carcass. When striped skunks and golden eagles

were fed a diet simulating toxin levels found in coyotes killed by LPCs, all study animals reduced their food intake, and half of the eagles showed sublethal signs of 1080 poisoning (Burns et al. 1991).

The other lethal techniques that show promise for selecting depredating coyotes – denning and calling and shooting – are both based on coyote calling. Calling has been in use for a long time (e.g. Alcorn 1946), and involves producing sounds that interest coyotes enough for them to vocally respond or approach. Calling techniques include imitating coyote howls and prey by mouth, making sounds with the help of small reed-based callers, or using sophisticated electronic speakers that store a variety of calls and can be operated by remote control. Denning typically depends on vocal responses to calling; these responses are used by trappers to pinpoint den sites. Once located, the den site is visited and pups or adults are killed; killing only the pups has been shown to temporarily reduce coyote depredations almost as much as killing the entire pack (Till and Knowlton 1983). Calling and shooting is used by itself or in conjunction with denning; coyotes are shot when they approach the site where a call was broadcasted. Calling is often used in conjunction with trained dogs that enhance responsiveness to calls and help damage control specialists find active coyote dens (Coolahan 1990). The selectivity of coyote calling towards breeding males seems to vary depending on the type of call used. Windberg and Knowlton (1990) found that calling and shooting was biased towards younger animals, but not sex-biased, when they used rabbit distress calls to attract coyotes. In contrast, Wagner (1997) found that calling and shooting was strongly sex-biased when pup distress calls, adult coyote calls, and trained dogs were used: 80 percent of coyotes shot were adult males despite an apparently equal population sex-ratio.

Coyote calling has potential as a selective, effective, and inexpensive way of dealing with problem animals. If used sparingly, denning and calling and shooting have no population-level or environmental effects, plus the public considers shooting to be much more humane than traps and poisons. The selectivity of these methods needs to be evaluated experimentally, and their use will remain limited without a more thorough understanding of how coyotes respond to a variety of calls played in different environmental conditions throughout the year.

A variety of common control methods can be used selectively in certain situations. Traps, snares, and M-44s can be set in locations that are more likely to be visited by problem animals (e.g. around sheep bedding grounds or coyote den sites); shooting can be used to kill coyotes as they approach bedded flocks; and aerial gunning can be used in conjunction with coyote calling to remove coyote dens. It is likely that these techniques will work well for selective control, but their efficacy remains to be demonstrated.

## **THE FUTURE OF COYOTE DEPRADATION MANAGEMENT RESEARCH**

Past and current research has improved our understanding of coyote ecology and assisted in the development of new and improved control methods, but this is not enough. New studies are needed that will examine coyote behavior and the efficacy of depredation management while following strict experimental protocols under operational conditions. It is essential that these studies be well designed, with appropriate controls and randomization. This level of rigor is rare in coyote depredation research, primarily because it is difficult to convince producers to accept a random treatment assignment that could require them to follow a strategy they feel is inappropriate. Much of their

resistance could probably be overcome with the establishment of a compensation fund for documented losses that occur when producers participate in research.

I believe that research needs to continue and expand along 4 fronts: (1) studies aimed at developing and improving depredation management techniques; (2) investigations of coyote ecology relative to livestock and natural prey; (3) comparative studies of the efficacy of specific control methods; and (4) examination of the relative costs and benefits of different control strategies in different situations. Specific ideas for research in each of these areas are outlined below. These experiments are not cheap or easy, but they would go a long way towards improving the success and cost-effectiveness of coyote depredation management.

### **Improved Depredation Management Techniques**

This category includes separate phases for technique development and testing. Development should begin with observations of coyote behavior towards control devices and procedures. For example, how do coyotes behave towards guard animals? What do they do after a behavior-contingent guard fires? What are the conditions that increase the responsiveness of dominant individuals to coyote calling? Which coyotes investigate traps set near bedding grounds? Observations and behavioral experiments investigating how marked, free-ranging coyotes behave towards various control methods are crucial for ensuring that techniques are as effective as possible before conducting expensive operational tests.

Operational testing should incorporate 2 or 3 pairs of sites that are identical with respect to important parameters (e.g. flock size, topography, herding procedures, depredation levels, and previous and ongoing control efforts). One site in each pair

should be randomly selected to receive the new control method, and the treatment site should be switched in the following year. Additional sets of sites that differ for some of the important parameters can be included in the experiment or pursued as a separate experiment to determine how the control technique performs across a variety of depredation management conditions. A standardized procedure for using the management technique and measuring its success would be needed to allow for comparisons of efficacy in different situations.

### **Investigations of Coyote Ecology**

A long-term (5 years or more) experiment is needed that investigates the relationship between coyote population density and depredation levels, examines potential buffering by wild prey, and determines whether depredation results from the actions of a subgroup of the coyote population. This study should be conducted at 2 or more sites, and planned to coincide with natural variation in wild prey abundance (e.g. a jackrabbit population irruption and crash, as in Stoddart et al. [2001]). Accurate counts of livestock losses from coyotes would be needed, and could be facilitated by using subcutaneous radio transmitters on a subset of the livestock so that causes of death of missing animals can be estimated. Prey densities can be measured using adequately calibrated line transects (for larger prey like rabbits) and trapping grids for rodents. Coyotes would not need to be captured for this experiment; mark-recapture population estimates can be obtained by analyzing DNA in coyote scats collected along a grid of scat transects. The DNA analysis would also allow for a determination of the social structure, especially if the data were supplemented with DNA from pup scats at den sites. Scat transects would also yield diet information and approximate territory boundaries for



coyotes in the population, plus the scat DNA can be compared with saliva DNA taken from the wounds of dead livestock (Williams et al. 2003) to identify the problem coyotes in the population.

### **Comparative Efficacy of Control Methods**

There are currently no solid data on the comparative efficacy of various corrective (i.e. post-depredation) lethal control methods, but this information can be collected with the cooperation of depredation management specialists. Participants would collect predator DNA from saliva samples on dead livestock, then carry out corrective control using methods of their choosing. These methods could include calling and shooting, denning, trapping with snares or leghold traps, use of M-44's, or corrective aerial gunning. As specialists kill coyotes in the area, they would collect a DNA sample from each carcass, note the control method, and record their location. DNA from saliva swabs would be matched to DNA from coyotes removed from the same area to determine whether the livestock killer was taken. This information would be supplemented with geographic habitat and topography data, plus information from livestock producers documenting important covariates (e.g. whether livestock are present year round, plus their numbers and distribution). Finally, a cost-benefit analysis of the various control techniques could be conducted using additional information concerning the time and physical resources used for control efforts.

### **Costs and Benefits of Different Control Strategies**

Several cost-benefit analyses suggest that lethal coyote control is a cost-effective way of solving depredation problems (Nass 1980, Pearson and Caroline 1981, Bodenchuk et al. 2000). These analyses were all based on the same group of studies from

the 1970's that documented livestock losses in situations with and without lethal control. The studies occurred in a variety of different habitats, with multiple types of husbandry practices, and differing baseline predation levels. As Pearson and Caroline (1981) noted, comparing these studies was not strictly valid but it did provide a reasonable starting point for estimating the benefits of predator control.

The accuracy of these and other cost-benefit analyses will be questioned until rigorous controlled experiments produce reliable data about different control strategies. One potential experiment would involve identifying 6 sites that are matched for animal husbandry practices, ecological characteristics, existing coyote control efforts, and livestock losses. At the start of the 3-year study, one third of the sites would receive no lethal control, another third would receive selective control targeted towards specific problem animals, and the remaining sites would receive coyote population reduction. Control methods would then be rotated for the next year (e.g. of the 2 sites initially receiving no lethal control, one would receive population reduction and the other would receive selective control), and the remaining treatment for each site would be applied in the final year. This counterbalanced repeated measures design should reduce any potential carryover effect, in which the treatment applied in one year affects the results for the following year (Zar 1999:259). Data collected would include livestock losses and the costs and efficacy of the different control strategies, and the analysis would produce the first accurate assessment of the benefits of lethal control for reducing livestock losses. Replicating this experiment at other groups of sites with different initial conditions would lead to an accumulation of reliable data that livestock producers and control agencies could use to determine the best depredation management strategy for a given situation.

## **Outline of the Dissertation**

The research projects outlined above clearly exceed the scope of a single dissertation. My goal is to tackle a small portion of the problem, by conducting research that will improve coyote depredation management through enhancing the selectivity and efficacy of coyote calling. This endeavor requires a better understanding of coyote behavioral ecology and vocal communication.

Chapters 2 and 3 explore the information content of coyote vocalizations. Coyotes may use vocalization characteristics to determine whether they know the calling animal, and they may also glean information about the distance to a sound's source. These characteristics may be altered by playback speakers or degraded by sound transmission. Chapter 2 therefore analyzes recordings of barks and howls to look for individually specific characteristics and Chapter 3 tests whether these features are detectable at distances up to 1 km from the sound's source. If individually specific cues are present in coyote vocalizations, then care must be taken when calling coyotes to ensure that vocalizations from a large number of coyotes are not used in one calling session – coyotes will be less likely to approach a playback if they think that they are going to face a large group.

Chapter 4 presents the results of a year of intensive playback trials. Important factors considered in evaluating responses to playbacks are: social status, location of coyotes and playback within the local territory structure, type of call used, and the effects of weather, season, and time of day. This chapter will help focus future research while providing a sound basis for understanding the selectivity of calling and shooting.

## **CHAPTER 2. INFORMATION CONTENT OF COYOTE LONG-RANGE VOCALIZATIONS: INDIVIDUAL DIFFERENCES IN BARKS AND HOWLS**

**Abstract:** The information content of coyote vocalizations is poorly understood, but has significant implications for behavioral ecology and wildlife management. Coyotes may recognize vocalizing individuals based on individual differences in acoustic characteristics. I investigated whether coyote barks and howls are individually distinctive using 293 barks and 280 howls recorded from 3 female and 4 male coyotes (4 captive breeding pairs). Coyote barks and howls both contained individually specific characteristics: discriminant analysis correctly classified the barks of 5 coyotes 69% of the time, the howls of 6 coyotes 79% of the time, and the howls of 4 males 87% of the time. Coyotes may take advantage of the presence of individually specific information within vocalizations by using simple gestalt models to facilitate recognition of familiar individuals.

**Key words:** bark, *Canis latrans*, coyote, discriminant analysis, howl, individual differences, information, vocalization.

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Despite decades of interest in using real or imitated coyote vocalizations for research and management (Alcorn 1946, Fulmer 1990, Beaudette 1996), there are no detailed studies of the potential information content of coyote vocalizations. Coyote long-range vocalizations are hypothesized to contain cues to the caller's identity, and may have characteristics useful for helping listeners localize a call's source (Lehner 1978). Showing that barks and howls include this information is the first step towards playback experiments documenting differential reactions of coyotes based on the acoustic

content of vocalizations. Responses that differ with the listener's sex or social status would have useful management implications. For example, alpha male coyotes may respond more aggressively to vocalizations of unknown coyotes than to neighbors, and their aggressive reaction could be used to attract and selectively kill a known problem animal. This chapter investigates whether barks and howls contain individually specific cues, and the subsequent chapter examines whether these cues are stable as they travel over distances up to 1 km from the source.

### **Coyote Long-Range Vocalizations**

McCarley (1975) first described coyote long-range vocalizations, and Lehner (1978) drew heavily on McCarley's report in his lexicon of coyote sounds. Coyotes use a graded communication system that transitions gradually from one type of vocalization to the next. This is a flexible system for indicating nuances of motivation and arousal, but it makes human categorizations of these signals somewhat arbitrary. Lehner (1978) recognized 5 long-distance vocalizations (Table 1), and I reduced this list to 4 by combining his bark-howl and howl into a single howl category. This reduction eliminated the subjectivity involved in using multiple categorizations for what amounted to a single graded vocalization, and it meant that each type of vocalization could be defined by strict acoustic criteria.

Barks were readily identifiable because they are a single burst of sound, always shorter than 0.2 seconds. Howls were any loud vocalization by a single individual that exceeded 0.3 seconds in duration. Howls therefore ranged over a broad continuum that included all of the gradations between short double-barks and long vocalizations that may have been frequency modulated. The group yip-howl was distinctive from a group howl;

a group yip-howl began when 1 or more of the participants switched from howling to continuous high-pitched yipping. The distinctive yips are apparent in Table 1 – the barks in the group howl have more harmonics and a much lower minimum frequency than the yips in the group yip-howl. For individuals, the relative proportion of barks to howls in a vocalization bout seemed to indicate the intensity of a coyote's mood: more howls indicated a higher level of excitement (B. R. Mitchell, personal observation).

### **Signature Vocalizations or Individual Voice Characteristics?**

Cues to the vocalizing individual's identity could occur in any vocalization type. These cues could take the form of signature vocalizations used by individuals as self-referential labels, or they could be voice characteristics based on physiology and personal preference. If humans used signature vocalizations to recognize individuals, we would only be able to recognize people when they stated their names. But people regularly recognize individuals – regardless of what is said – based on relatively constant voice characteristics like pitch, accent, and talking speed. In fact, one recent study (Bachorowski and Owren 1999) successfully used discriminant analysis to classify sex and identity for 125 people based on part of a single vowel sound.

Until researchers can ask their study animals whether they rely on vocal signatures or voice characteristics to recognize individuals, the distinction essentially reduces to semantics and researcher perspective. McCowan and Reiss (2001), while critiquing vocal signatures, wrote that discrimination by signature calls predicts “that each dolphin produces, and is individually identified by, a categorically different stereotypic whistle contour type, and not by individual acoustic variations of a shared contact whistle or call type”. The distinction that McCowan and Reiss were making is an

artificial one that depends solely on the level of difference between 2 spectrograms that a researcher decides is “categorically different”. Thus where one observer sees 2 completely different types of calls that are not shared between individuals, another may see a single call type that exhibits variability between individuals. It is not surprising that McCowan and Reiss (who believe that dolphins have individual voices) found no evidence of signature whistles when they replicated a vocal signature experiment conducted by other researchers. Lambrechts and Dhondt (1995) echoed these sentiments, noting that the way songs were classified determined whether 2 birds had different repertoires or merely sang different renditions of the same songs. Similarly, Owren and Rendall (2001) argued that researchers should not make assumptions about the presence of referential information like vocal signatures; instead they should focus on analyzing vocalizations from the perspective of their form and function.

While there is no functional difference between signature calls and individual voice, I lean towards the use of voice characteristics as the mechanism for individual recognition in most animals. In other words, coyotes do not howl their names; rather, they howl to convey their mood and individual information happens to be present as well.

### **Individual Differences in Animal Vocalizations**

Regardless of the theoretical approach used, individual vocal characteristics have been documented in a variety of species, from birds (Peake et al. 1998, Walcott et al. 1999) to various mammalian orders including primates (Dallmann and Geissmann 2001), ungulates (Reby et al. 1999), rodents (McCowan and Hooper 2002), elephants (McComb et al. 2000), whales (McCowan and Reiss 2001), seals (Phillips and Stirling 2000), and carnivores (McShane et al. 1995, Holekamp et al. 1999). Numerous studies have taken

the additional step of showing that individuals actually do discriminate between different conspecifics. Examples of animals using individual vocal cues can be found in birds (Jouventin et al. 1999), primates (Cheney and Seyfarth 1980, Weiss et al. 2001), elephants (McComb et al. 2003), whales (Sayigh et al. 1999), and seals (Charrier et al. 2002). Within the wild canids, individual differences have been documented in swift foxes (Darden et al. 2003), African wild dogs (Hartwig 2003), wolves (Theberge and Falls 1967, Tooze et al. 1990), and possibly dholes (Volodin and Volodina 2002). Frommolt et al. (2003) documented individuality in barks of a territorial population of arctic foxes and also showed that foxes respond differently to barks from members of their own social group than they do to other foxes.

Cues to sex or identity have never been demonstrated for coyote vocalizations, perhaps because of the high amount of intra-individual variability in their howls. I tested whether coyote barks and howls contain individually specific cues by examining multiple vocalizations recorded from known individuals. Vocalization characteristics were then measured and analyzed using discriminant analysis. I predicted that discriminant models would demonstrate the presence of individually specific cues by successfully classifying vocalizations to the correct individual.

## **METHODS**

### **Recording and Sound Processing Procedures**

*Utah Recordings.*--Recordings were collected at the US Department of Agriculture, Wildlife Services, National Wildlife Research Center (NWRC) field station in Logan, Utah, between 8 July 1998 and 27 July 1998. I used a Tascam DA-P1 digital tape recorder (DAT) (TEAC America, Montebello, CA) with a phantom powered Sennheiser



MKH 70 shotgun microphone (Sennheiser Electronic Corporation, Old Lyme, CT) at a recording height of 1.0 m.

I intended to collect recordings faster by eliciting vocalizations from subject animals using playbacks of locally recorded howls. I recorded group howling from the NWRC kennel (housing approximately 75 coyotes), and spontaneous lone howls from a male coyote in a 0.1-ha pen near the animals used in the study. These stimuli were digitized through the sound card on a laptop computer using Sound Forge 4.5 (Sonic Foundry, Madison, Wisconsin, USA).

Subject animals were all housed as breeding pairs in 0.1-ha “clover” pens, so named because each set of 3 rounded pens was connected to a central observation building. The adjoining portion of each pen was a concrete wall, but the rest of each enclosure was chain-link fence. The coyotes had been housed in these pens for over 6 months, and had not been involved in any behavioral research. These coyotes were the only individuals isolated enough to allow for clean recordings. Out of 9 possible pairs of study animals, 3 pairs were excluded because the microphone and speaker cables could not reach the middle clover pen in each set. Another pair was excluded because the female had been kept as a pet for most of her life (although the male’s spontaneous vocalizations were used as playback stimuli), and a final pair was excluded later in the study after neither animal vocalized for an entire day. One member of each of the pairs was marked with an orange livestock marker to facilitate discrimination of individuals. Details about the 8 study coyotes are presented in Table 2.

The microphone was set up outside of the observation building, with a 15-m cable connecting it to the DAT inside the building. The playback equipment – a set of Audix

PH-3 speakers (Audix Corporation, Wilsonville, Oregon, USA) – was placed on the ground near the microphone, and a 15-m cable connected them to the laptop computer inside the building. I remained inside the observation building for the duration of each recording session, and recorded audio observations of vocalization behavior using a lapel microphone connected to the second channel of the DAT.

There were typically 2 recording sessions per day, during times when the coyotes vocalized regularly and were visually identifiable. The morning session began at 0615 (shortly before dawn) and lasted until an hour passed with no vocalizations, and the second session began at 1945 and lasted until 2115 (just after sunset). On any given day, only 1 pair of coyotes was recorded. Stimuli were played to subject animals every half-hour, but subjects never responded directly to the recordings. The playbacks did, however, usually encourage animals in the nearby kennels to vocalize, and subject animals often responded to the kennel howls. During recording sessions I recorded all spontaneous and indirectly elicited vocalizations, while making observations about which coyote of the subject pair was vocalizing.

*Sound Processing.*--Recordings were digitized at a 25-kHz sample rate using DiskRec 1.0 (Engineering Design, Belmont, Massachusetts, USA) and a 50 kHz Dart Digital Signal Processor card (Engineering Design, Belmont, Massachusetts, USA). With the help of Signal 3.0 sound analysis software (Engineering Design, Belmont, Massachusetts, USA), I isolated and saved vocalizations along with the identity of the vocalizing subject when that could be determined.

Of the 1,754 vocalizations I saved, 641 contained single vocalizations (318 barks and 323 howls) by known individuals. Because this data set was also used in a study of

the effects of distance on vocalization parameters (Chapter 3), 57 of the recordings were removed because they could not be used in the distance experiment (see Chapter 3 methods). An additional howl was removed because background noise interfered with spectrogram measurements, and 10 other howls were removed because they were made by individuals that contributed less than 15 vocalizations each. The final vocalization library contained 293 barks (from 2 females and 3 males) and 280 howls (from 2 females and 4 males).

### **Bark Measurements and Variables**

Each bark was assigned a random number, generated using Excel 97 (Microsoft, Redmond, Washington, USA). For all discriminant analyses the vocalizations were separated into appropriate groups (sexes or individuals). The 75% of vocalizations within each group that had the highest random numbers were used as training data, and the remaining vocalizations were used as test data.

*Spectrogram Measurements.*--A spectrogram of each bark was displayed using Signal 3.1. Spectrograms are graphical plots of sounds, with time on the x-axis, frequency on the y-axis, and intensity represented by darker shading (e.g. Table 1). All bark spectrograms were created using 512-point Fast Fourier Transforms (FFTs), a 0.25 ms increment between FFTs, and a maximum frequency of 4 kHz. The resolution of the cursor used to record measurements was 0.43 ms and 17 Hz. On each bark spectrogram, research associate Maja Makagon recorded the start and end time of the bark, the bark structure (chaotic or harmonic), and the harmonic structure (frequency contour shape) of the bark (Figure 1). Bark start and end times were converted to duration (end minus start). Bark structure was rated on a 3-point scale: “1” for chaotic (no harmonics), “2” for

intermediate (faint harmonics), or “3” for harmonic barks. The harmonic structure was rated on a 5-point scale based on measurements of the lowest (fundamental) harmonic: “1” for chaotic barks; “2” for flat barks, where the frequency increase across the fundamental was less than 100 Hz; “3” for angled barks, where the frequency increase was more than 100 Hz; “4” for peaked barks, where the middle of the fundamental was more than 100 Hz higher than both ends; and “5” for strongly peaked barks, where the middle of the fundamental was more than 200 Hz higher than both ends.

*Power Spectrum Measurements.*--I wrote a batch processing program for Signal 3.1 that generated a power spectrum for each bark. The power spectrum of a sound is a graph of average amplitude at each frequency for a given slice of time (a spectrogram is essentially a series of power spectra or FFTs for different times). These spectra were generated using a 16-k FFT length, and smoothed using a 100-Hz moving average. The program recorded the maximum amplitude and the frequency of maximum amplitude for each smoothed spectrum at a resolution of 1.5 Hz and less than 0.01 dB-volts (Figure 2).

*Spectral Moments.*--Using methods similar to those of Forrest et al. (1988), I wrote a Signal program to calculate the first four spectral moments (mean, standard deviation, skewness, and kurtosis) of each bark (Figure 3). For this procedure I resampled and anti-alias filtered the barks to a 12-kHz sample rate using Sound Forge 6.0. Resampling allowed me to take advantage of the digital bandpass filter in Signal 3.1 to remove background noise below 300 Hz and above 4 kHz. Without resampling, the lowest frequency retained by the filter would have been 625 Hz (1/40 of the sample rate), which was well within the typical region of bark spectral energy. For each bark, the program bandpass filtered the sound and then selected an 80-ms segment centered on the time of

maximum sound amplitude. The segment was divided into 7 regions, each 20-ms long and overlapping 50% of the next region. For each region, a 256-point FFT was calculated on a linear scale; each point of the FFT represented the sound amplitude over a 46.9-Hz portion of the region. The FFT could then be treated as a discrete probability distribution, and moments calculated according to the formulas given in Forrest et al. (1988). The mean, standard deviation, skewness, and kurtosis of each bark were estimated by averaging the moments for each of the seven bark regions.

*Harmonic-to-Noise Ratio.*--I also calculated an estimate of the Harmonic-to-Noise Ratio (HNR) of the barks using methods similar to Riede et al. (2001). This measure estimated the noisiness of each bark by subtracting a power spectrum that had been smoothed (and therefore represented the overall noise-print of the vocalization) from the original power spectrum (which emphasized the periodic harmonic nature of the sound). The maximum difference between the 2 spectra is the HNR, which is a ratio because subtraction on the logarithmic dB scale is equivalent to division on a linear scale. My HNR program selected the 50-ms segment of each bark that was centered on the point of maximum sound amplitude. Then each segment was divided into 7 regions, each 20-ms long and overlapping 75% of the next region. A 512-point FFT was calculated for each region, and then all 7 FFTs were averaged to produce the harmonic spectrum. A copy of the harmonic spectrum was then smoothed using a 10-point (488-Hz) moving average to produce the noise spectrum. Values below 500 Hz and above 4 kHz were removed from both spectra, and then the noise spectrum was subtracted from the harmonic spectrum. The HNR was converted to a linear scale, and then the HNR (in volts) and HNR frequency (in Hz) were recorded (Figure 4).

## Howl Measurements and Variables

As with the barks, each howl was assigned a random number to determine which howls would be included in discriminant analysis training sets, and which would be used for testing the discriminant model.

All howl measurements were made on spectrograms produced in Signal 3.1 from 25-kHz audio files. Spectrograms were displayed using a 5-ms step between successive FFTs and a 1,024-point FFT size. Spectrograms were zoomed to approximately 1 second by 1 kHz for measurement, and measurement resolution was at or better than 1.7 ms and 5.0 Hz.

*Time and Frequency Measurements.*--Time and frequency measurements were taken at 5 points along the fundamental for each howl: the howl's start, the end of the howl's rising portion, the point of maximum frequency, the start of the howl's falling portion, and the end of the howl (Figure 5). The frequency and time measurements were converted into duration (measured in ms) and slope (measured in Hz/ms) variables: 1) of the rising portion; 2) from the start of the middle portion to the maximum frequency; 3) from the maximum frequency to the end of the middle portion; and 4) of the falling portion. These 8 variables were used along with the frequency measurements in the statistical analyses.

*Howl Type.*--Each howl was assigned a howl type between 1 and 5 based on frequency measurements and the time of maximum frequency: "1" for howls with a midsection that increased more than 100 Hz, "2" when the midsection peaked in the second half at a value more than 100 Hz above both ends, "3" for a flat howl showing less than 100 Hz of change in the midsection, "4" when the midsection peaked in the first half at a value more than 100 Hz above both ends, and "5" for howls with a midsection that decreased

more than 100 Hz. The 100-Hz criterion was an arbitrary value that corresponded to an easily recognized frequency change.

*Howl Irregularities.*--Maja Makagon and I documented nonlinear phenomena of howl spectrograms, specifically subharmonics (Figure 6) and noisy sections (also called “deterministic chaos” [Fitch et al. 2002]). Nonlinearities were ignored if they were less than 50 ms in duration or 100 Hz in bandwidth, since smaller features were difficult to differentiate from background noise. If 1 type of nonlinear phenomenon graded directly into another type (such as a segment of deterministic chaos transitioning into a section with subharmonics), we counted 2 features rather than one. We recorded the number of nonlinear phenomena in the rising, middle, and falling portions of each howl.

We measured frequency modulation of howls by documenting frequency shifting and wavering (Figure 6). Frequency shifts were found in the middle section of a howl and were fairly abrupt changes in the average frequency. To be counted as a frequency shift, the change had to be at least 50 Hz, could not be part of a waver, and could not return to the original frequency for at least 400 ms. Wavers were short frequency-modulated sections that often gave coyote howls a distinctive “warbling” sound. Wavers had to be less than 400-ms long, and had to show a frequency drop of at least 50 Hz relative to the start and end of the waver. I chose a frequency change threshold of 50 Hz because this was a level of change that I could detect when listening to vocalizations. Similarly, the 400 ms transition from waver to frequency shift corresponded with the duration where wavers no longer had a “warbling” sound.

For each howl, we recorded the number of frequency shifts between 50 and 100 Hz, and the number of shifts greater than 100 Hz. Wavers were classified according to

location (rising portion or middle of the howl) and amplitude (50 to 100 Hz, 100 to 200 Hz, or greater than 200 Hz). Wavers in the rising portion of the howl were also counted if their amplitude was between 0 and 50 Hz.

### **Discriminant Analysis**

*Assumptions.*--I used linear discriminant analysis to examine whether bark and howl variables could be used to tell individuals apart. Discriminant analysis classifies observations into one of several categories by generating a linear combination of variables that best predicts group membership (Selvin 1995:172). The assumptions of multivariate normality and equal covariance matrices were never met, but discriminant analysis is robust to violations of these 2 assumptions (Klecka 1980, Selvin 1995:177). The assumption of independence was more problematic, since it was potentially violated by my data collection procedures and because discriminant analysis is sensitive to independence violations (Selvin 1995:177). My data set included numerous cases of temporally close vocalizations, and these cases violated independence to the extent that adjacent vocalizations from an individual were temporally autocorrelated. I found slight evidence of temporal autocorrelation in the bark data and no evidence in the howl data (Appendix 2); it is highly unlikely that such a small departure from independence would have affected the results.

Many researchers suggest excluding a variable if it is highly correlated with other variables in the analysis, but threshold correlation levels vary from 0.8 (Kazial et al. 2001) to 0.95 (Gouzoules and Gouzoules 2000). I used 0.9 for my threshold, which resulted in excluding bark skewness from the analysis due to high correlations with mean ( $r = -0.91$ ) and kurtosis ( $r = 0.94$ ).



Discriminant analysis also performs poorly when there is no variability within a group (Klecka 1980), so I excluded variables when multiple groups (individuals or sexes, depending on the analysis) showed no variability. In addition, discriminant analysis should not have “grossly different” group sizes (Klecka 1980) and the number of variables should be less than 0.33 times the number of observations (Kazial et al. 2001). The ratio of the largest to smallest group size was never more than 3.7 for bark and 4.4 for howl analyses, and the only analysis with too many variables involved discriminating 2 individual females based on 31 howls. In this situation, I chose up to 10 variables based on the significance of univariate t-tests for each potential variable.

*Procedures.*--Discriminant analysis is an inferential technique based on sample data, and validation of the model is typically based on the same data used to create the model. Therefore the classification accuracy is generally an overstatement of the discriminant analysis' true success (Klecka 1980). This bias can be countered with split-sample validation, where a portion of the data is withheld and used to check the model that was built using the rest of the data. There is no hard criteria for the size of the split; Gouzoules and Gouzoules (2000) withheld 25% of their data, Riede et al. (2001) reserved 50%, and Tooze et al. (1990) held back 40% of their observations from 5 of 6 individuals. I reserved 25% of my vocalizations for split-sample validation.

All discriminant analyses were conducted using SYSTAT 9.0 (SPSS, Chicago, Illinois, USA). For each analysis, I sorted the vocalizations by group and random number, and excluded the first 25% of each group's observations. These excluded data became the “test” data used to check the “training” data from the analysis. I tried both forwards and backwards stepwise variable selection, and selected the most parsimonious

model unless a more complicated model showed a dramatically higher classification accuracy. I used an F-to-enter and F-to-remove probability of 0.15, and a tolerance of 0.01. SYSTAT provided stepwise model selection and detailed statistical output, but could not perform the split-sample validation. Consequently, the discriminant model was re-created using the MANOVA platform of JMP IN 4.0 (SAS Institute, Cary, North Carolina, USA), and the discriminant functions were then applied to the test data.

I computed kappa and its associated 95% confidence interval for each classification according to the procedure in Titus et al. (1984). Kappa adjusts the percentage accuracy of discriminant analyses to account for chance and the effect of unequal group sizes. For example, a raw classification accuracy of 50% is good if there are 10 groups in the analysis, but it is no better than chance if there are only 2 groups; whereas a kappa of 0.50 indicates that the model made 50% fewer errors than expected based on chance, regardless of the number of groups or the group sizes. As with raw classification accuracies, estimates of kappa were biased to higher values for training data sets; kappa is only unbiased with test data that were not used to develop the classification model (McGarigal et al. 2000:167-8). However, estimates of kappa were less precise for the test data because of smaller sample sizes, and this led to multiple instances where kappa was lower for the training data. In the text I have reported the lower of the 2 estimates of kappa; both estimates can be found in the tables along with their 95% confidence intervals.

I used discriminant analysis to classify barks and howls to the individual that produced them. Because the presence of sex-specific information in vocalizations can change classification accuracy and alter the importance of different variables

(Bachorowski and Owren 1999), I also used discriminant analysis to classify female barks and howls to the individual female and male barks and howls to the individual male.

## **RESULTS**

### **Bark Analyses**

Raw bark data showed ample among-individual variation for discriminant analysis to work with (Table 3). All the variables – with the possible exception of maximum dB level – differed markedly between individuals.

*Classifying Barks to Individual.*--Both stepwise variable selection procedures converged on a discriminant model containing all variables except bark structure, maximum dB frequency, and HNR frequency. The eigenvalues were used to calculate the relative proportion of total discriminating power accounted for by each discriminant function. The first function was 3.5 times more useful than the second function, and the last 2 functions only accounted for 10% of the model's discriminating power. The squared canonical correlations were high for the first 2 functions (the identity of the barking individual explained 65% and 35% of the variability in the first and second function, respectively). Even though the last 2 functions had low relative proportions and squared canonical correlations, all of the discriminant functions were statistically significant (Table 4).

Within each discriminant function, the absolute values of the standardized coefficients reflect the importance of the variables. The discriminating power of the first function was primarily due to the higher order spectral moments (standard deviation and

kurtosis), bark loudness, and duration. The second discriminant function was primarily influenced by differences in mean frequency and duration (Table 5).

The classification accuracy of the training data was good, with an overall 72% accuracy that ranged between 58% and 81% for each individual. These results are best displayed as a classification matrix, where the columns represent model predictions for cases in each row (Table 6). The most common mistake was confusion of mated coyotes M-5416 and F-5471 (21 out of 62 total mistakes). The test data classification showed a lower overall accuracy, and more variability in individual success rates (Table 7). The corresponding kappa estimates were  $0.63 \pm 0.08$  ( $\bar{x} \pm 95\%$  CI) for the training data and  $0.58 \pm 0.14$  for the test data, indicating a classification success about 60% better than chance.

*Male and Female Analyses.*--Analyzing the 2 females and 3 males separately led to models with high raw accuracy scores, but low chance-corrected test model accuracies. The female-only model included duration, bark structure, max dB frequency, kurtosis, and HNR, while the male-only model included duration, bark harmonic structure, mean, and kurtosis. The female-only model was 97% accurate classifying 91 training barks and 87% accurate classifying 31 test barks, with corresponding kappa estimates of  $0.91 \pm 0.10$  ( $\bar{x} \pm 95\%$  CI) and  $0.59 \pm 0.38$ . The male-only model was 79% accurate classifying 128 training barks and 72% accurate classifying 43 test barks, with kappas of  $0.67 \pm 0.11$  ( $\bar{x} \pm 95\%$  CI) and  $0.53 \pm 0.22$ , respectively.

## Howl Analyses

Individual means for the howl variables differed markedly by individual (Table 8). This indicated that there was plenty of variation for discriminant analysis to use for classifying the different study animals.

*Classifying Howls to Individual.*--I chose the forwards stepwise model because it used fewer variables and had a similar accuracy when compared to the backwards stepwise model. The summary statistics for the discriminant functions (Table 9) showed that the first function was twice as useful as the second, and 5 times as useful as the third. These first 3 functions accounted for 95% of the model's discriminating power. The fourth function was not particularly useful, but it added statistically significant discriminating power. The final function was not useful or statistically significant. The high squared canonical correlations of the first 3 functions suggested that they would be very successful at classifying individuals.

The variables contributing most strongly to the first discriminant function were maximum frequency, end frequency, rise slope, and 50-Hz to 100-Hz rise wavers. The second function was most strongly affected by fall slope, with help from the slope from the maximum frequency to the start of the fall, nonlinearities in the fall, and 50-Hz to 100-Hz wavers in the middle of the howl (Table 10). Except for end frequency, the first function appeared to favor characteristics of the beginning of the howl, while the second function related more to characteristics of the howl's middle and end. Classification accuracy for the training data was good, with an overall 79% accuracy and a chance-corrected accuracy of  $0.74 \pm 0.07$  ( $\bar{x} \pm 95\%$  CI). Accuracy for specific individuals varied from 53% to 90% (Table 11); the 53% accuracy corresponded to the coyote with the

second-lowest number of howls – only 17 were used in the training data. The next-lowest individual accuracy was 77%. The most common classification errors involved the females: 19 of 44 errors were cases where males were classed as one of the females, and 10 of the errors involved a female being classified as one of the other animals. The analysis evidently included too few howls from the females (14 from F-5438 and 17 from F-5414) for the discriminant functions to fully model their variability. Another 6 errors were M-5430 howls that were misclassified to his brother (M-5429).

The discriminant model incorporating all individuals did even better with the test data than with the training data. Overall accuracy was 83% – with a corresponding kappa of  $0.79 \pm 0.11$  ( $\bar{x} \pm 95\% \text{ CI}$ ) – and individual accuracies varied between 60% and 100% (Table 12). Out of 12 classification errors for the test data, 7 involved M-5430 being classified as a female and 4 were due to a female being classified as another individual.

*Male and Female Analyses.*--The discriminant model for the 4 males performed better than the model incorporating all individuals. The male-only training accuracy was 87% and the test classification accuracy was 92%, with corresponding kappas of  $0.82 \pm 0.07$  ( $\bar{x} \pm 95\% \text{ CI}$ ) and  $0.89 \pm 0.09$ . The trend for discriminant analysis to confuse the two brothers (M-5429 and M-5430) was even stronger in the males-only howl analysis, where 11 of 23 errors in the training data set and 4 out of 5 errors in the test data set involved confusion of these 2 animals. Plotting the values of the first discriminant function against values of the second emphasized the similarity between the brothers: they were completely indistinguishable based on the first two functions (Figure 7).

The model based on the 2 females performed worse than the other models. The 87% training and 82% test accuracies compared favorably to the model for all

individuals, but because there were only 2 females and a small sample size (31 training howls) the kappa estimates were low and had large confidence intervals:  $0.74 \pm 0.24$  ( $\bar{x} \pm 95\% \text{ CI}$ ) for the training data and  $0.62 \pm 0.48$  for the test data.

## **DISCUSSION**

### **Information Content of Animal Vocalizations**

Animal sounds regularly contain cues that are sexually or individually specific. One source of these cues stems from the physiology of sound production. The source-filter model of animal acoustics says that the fundamental frequency of animal vocalizations is determined by characteristics of the sound's source – the larynx. Laryngeal muscle tension and the amount of air pressure from the lungs can be varied to alter the fundamental frequency. The acoustic energy generated by the larynx is then modified by an acoustic filter whose properties are determined partly by the length, shape, and volume of the supralaryngeal vocal tract (consisting of the pharynx, oral cavity, and nasal cavity). Certain frequencies (the formants) are passed with minimal filtering, while other frequencies are strongly curtailed (Rubin and Vatikiotis-Bateson 1998).

Because features of the larynx and the overall length of the vocal tract are strongly correlated with body size, sex differences should be detectable whenever species are sexually dimorphic and acoustic cues to these features exist. Bachorowski and Owren (1999) used this reasoning and were 99% accurate when they employed discriminant analysis to classify the sex of 125 humans. Their analysis was based on only 2 characteristics: the fundamental frequency and an estimate of vocal tract length that was derived from the first 3 formants. These researchers then used acoustic characteristics

associated with both the sound source and filter to accurately classify 76% of their sounds to the correct individual.

Vocalizations with cues to sex and identity should be the rule rather than the exception, but the reality is that not all calls are useful for detecting physiological cues. Calls with low fundamental frequencies and calls with low-amplitude wideband noise are best for revealing body size and individuality (Owren and Rendall 2001). And although minimum fundamental frequency is constrained by physiology, many mammals can produce a broad range of fundamental frequencies by varying the rate of vocal fold vibration. When they use a high fundamental frequency or sound amplitude, aspects of the individually-specific acoustic filter are difficult to detect (Owren and Rendall 2001). Canid growls contain highly specific cues to size (Riede and Fitch 1999) and probably identity, but barks (with their high sound amplitudes) and howls (with their high fundamental frequencies) are less likely to encode this information.

### **Individually Specific Cues in Coyote Vocalizations**

Coyote vocalizations clearly contained individually specific characteristics. The barks of 5 individuals were correctly classified about 70% of the time (a 58% chance-corrected accuracy), and the howls of 6 individuals were correctly classified almost 80% of the time (a 74% chance-corrected accuracy). Individual vocal tract morphology was not expected to leave a large imprint on barks because their high amplitude should mask much of the physiological influence (Owren and Rendall 2001). Some of this influence should remain, though, and I suspect that many of the individual differences in spectral moments were due to differences in vocal tract morphology and sound filtering. The individual differences among the remaining bark variables were likely due to personal



preference and habit. For example, duration and maximum dB level of barks may be controlled by decisions about the volume and expulsion rate of air used to form the vocalization. The high frequency of confusion between barks of the mated pair F-5471 and M-5416 is likely due to chance, but it could potentially be due to intentional bark matching by the pair.

Howls should be even less affected than barks by individual variation in vocal tract morphology because of their relatively high fundamental frequency (Owren and Rendall 2001). Frequency measurements could have been loosely related to individual differences in larynx morphology by representing the range over which each individual was able to comfortably vocalize. Nonlinear phenomena might have a physiological basis if the threshold controlling the transition to nonlinear features varied in different coyotes. However, the majority of howl features that were important for discriminating individuals should be under conscious control. These include the duration of the fall, various slope measurements, and the presence of wavers.

Individual coyotes appear to be born with or develop a preference for howling in a certain way, and this preference is likely constrained over time into a habitual and individually specific howling technique. My results suggest that at least some of this preference has a genetic basis, because the pair of same-sex siblings I recorded had howls that were commonly confused and close together in discriminant space. Pups at the NWRC field station were removed from their mothers soon after birth and raised according to standard protocols with other pups at the facility, so it is unlikely that the sibling similarity was learned in a shared family environment.

### **Do Coyotes Use Multivariate Statistics?**

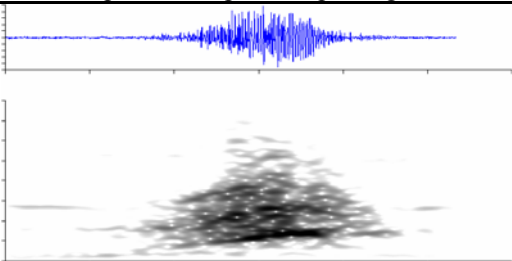
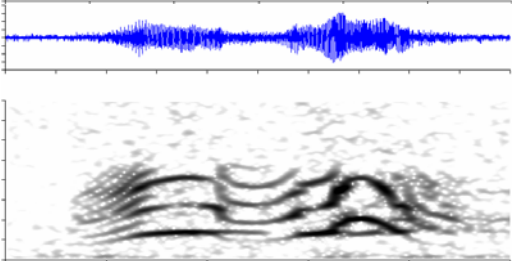
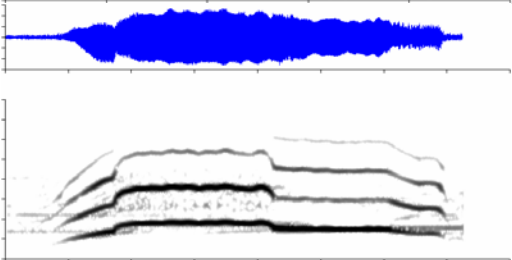
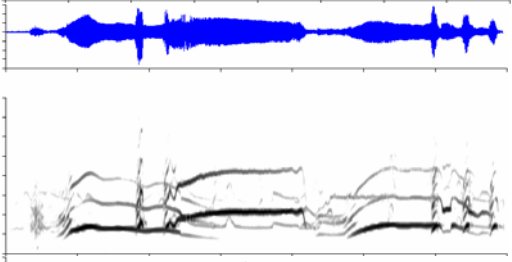
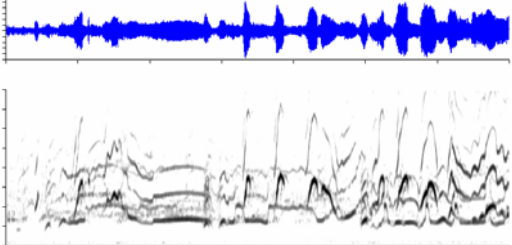
Coyotes probably do not perceive individual howl and bark characteristics in a way that even remotely compares to measurements on spectrograms or power spectra. They certainly do not classify howls using complex multivariate statistics. So although discriminant analysis has shown that coyote vocalizations contain individually-specific features, this is not proof that coyotes are able to recognize individuals based on barks or howls. But there is information present in the vocalizations, and there are compelling reasons to expect that using this information would be advantageous for coyotes. Individual recognition would allow coyotes to recognize and respond to their mates, who may be advertising danger, a desire to reunite, or the presence of food. Recognizing neighbors would be useful for limiting the effort expended in territory maintenance, because after initially settling on boundaries coyotes could generally ignore howls from neighboring territories. Territorial activity would then only be needed if known neighbors started encroaching or if they were replaced. Recognizing neighbors might also allow coyotes to eavesdrop on agonistic interactions, and evaluate their chances of succeeding against a new competitor. Hearing unknown individuals could signal a need to closely evaluate and repulse a threatening rival, or indicate the presence of a potential mate.

Coyotes probably lack the detailed analytical capability of statistical software, but they should be capable of building simple gestalt mental models of the vocalizations of different individuals. It is unlikely that these mental models would be as accurate as statistical ones, but coyotes have an advantage that discriminant analysis does not: they can use an entire vocalization bout to determine a caller's identity. So even if some

howls are ambiguous, it is likely that a few howls in the bout would be clearly representative of the vocalizing individual. Coyotes should also be able to integrate other information into their classification, such as bout-level variables (e.g. spacing between vocalizations) and the approximate location of the signaler.

Fulmer (1990) found no difference in free-ranging coyote responses to their own, neighbor, and non-neighbor vocalizations. However, her non-neighbor vocalizations were recorded on-site and were probably still familiar animals, her stimuli consisted of only 4 howls and no barks, and her playbacks were conducted between mid-April and mid-August, when coyotes were more likely to be interested in provisioning pups than aggressively defending their territories. A more appropriate test of the ability of coyotes to discriminate individuals could be accomplished with a habituation-discrimination experimental design (where a researcher habituates captive coyotes to howls from one individual, then switches the individual and sees if the animals' behavior changes) or with an experiment that rewards coyotes for making correct discriminations. Field playbacks using vocalizations from known and foreign individuals could also be used to test coyote discrimination ability, but would be much more challenging.

Table 1. Coyote long-range vocalizations.<sup>1</sup>

Vocalization	Amplitude Graph and Spectrogram <sup>2</sup>	Description
Bark		Short duration, high amplitude vocalization; energy distribution varies from chaotic to harmonic. Probably a low to medium intensity threat or alarm vocalization. The acoustic structure may make it easy to locate, especially when uttered in series.
Bark-Howl		Short frequency-modulated vocalization that develops from barks that are strung together. Usually preceded by 1 or more barks. Probably a high intensity alarm or threat. Its acoustic structure may make it easy to locate.
Howl		High-amplitude vocalization with slight to moderate frequency modulation. Often preceded by barks. Probably facilitates reunions with pack members. The large intra-individual variability in howls may make it hard to demonstrate inter-individual differences.
Group Howl		Multiple individuals producing lone howls at the same time or in alternation. Probably facilitates reunions, likely a low to moderate display for reinforcing group bonds and announcing territory occupancy.
Group Yip-Howl		High amplitude and intensity vocalizations involving multiple individuals howling and yipping together in a complex pattern. Likely a high intensity display for reinforcing group bonds and announcing territory occupancy.

<sup>1</sup> According to Lehner (1978). In this dissertation, bark-howls and howls are combined as howls.<sup>2</sup> Amplitude graphs show relative sound volume over time. Spectrograms show frequency over time; frequency (y-axis) is 0 to 4 kHz and time (x-axis) is 0.3 s for the bark, 0.5 s for the bark-howl, 1.6 s for the howl, and 7 s for the group howls.

Table 2. Sample sizes, sex, age, weight, and relationships for coyotes at the NWRC Logan Field Station, July, 1998.

Coyote	Barks <sup>1</sup>	Howls <sup>1</sup>	Sex	Age	Weight (kg)	Mate	Sibling(s)
F-5414	--	23	F	3	11.0	M-5320	F-5415 & M-5416
F-5415	--	--	F	3	10.4	M-5430	F-5414 & M-5416
F-5438	26	19	F	3	9.1	M-5429	
F-5471	96	--	F	2	8.4	M-5416	
M-5320	91	55	M	5	15.0	F-5414	
M-5416	52	61	M	3	14.4	F-5471	F-5414 & F-5415
M-5429	28	39	M	3	14.8	F-5438	M-5430
M-5430	--	83	M	3	12.5	F-5415	M-5429

<sup>1</sup> Sample sizes used in discriminant analyses. Dashes indicate fewer than 15 vocalizations and exclusion from analyses.

Table 3. Bark data for coyotes recorded at the NWRC Logan Field Station, July, 1998.<sup>1</sup>

Variable	F-5438	F-5471	M-5320	M-5416	M-5429
Duration (ms)	135 ± 3.3	109 ± 1.7	129 ± 1.7	116 ± 2.3	139 ± 3.2
Bark Structure	2.23 ± 0.12	1.91 ± 0.06	1.70 ± 0.07	2.00 ± 0.09	1.07 ± 0.12
Bark Harmonic Structure	3.46 ± 0.25	2.75 ± 0.13	2.52 ± 0.14	3.25 ± 0.18	1.14 ± 0.25
Max Db (dB-volts)	-42.6 ± 1.12	-43.1 ± 0.58	-42.6 ± 0.60	-46.2 ± 0.79	-47.2 ± 1.08
Max dB Frequency (Hz)	878 ± 48	723 ± 25	705 ± 26	893 ± 34	919 ± 47
Mean (Hz)	1,220 ± 22	1,295 ± 11	1,108 ± 12	1,328 ± 16	1,380 ± 21
Standard Deviation (Hz)	624 ± 14	705 ± 7.2	594 ± 7.4	681 ± 9.8	658 ± 13
Skewness	1.67 ± 0.07	1.28 ± 0.04	2.01 ± 0.04	1.25 ± 0.05	1.19 ± 0.07
Kurtosis	3.95 ± 0.30	1.74 ± 0.16	5.73 ± 0.16	2.23 ± 0.21	2.15 ± 0.29
HNR (volts)	10.57 ± 0.76	8.67 ± 0.40	8.35 ± 0.41	6.49 ± 0.54	3.13 ± 0.73
HNR Frequency (Hz)	806 ± 56	719 ± 29	709 ± 30	728 ± 39	867 ± 54

<sup>1</sup> Values are mean ± standard error. Sample sizes: 26 from F-5438, 96 from F-5471, 91 from M-5320, 52 from M-5416, and 28 from M-5429.

Table 4. Discriminant function statistics from analysis of individual differences in barks.

Function	Eigenvalue	Relative Proportion	Squared Canonical Correlation	X <sup>2</sup> , DF	p(X <sup>2</sup> )
1	1.8828	0.692	0.653	374.29, 28	< 0.0001
2	0.5470	0.201	0.354	149.76, 18	< 0.0001
3	0.1735	0.064	0.148	57.29, 10	< 0.0001
4	0.1165	0.043	0.104	23.35, 4	= 0.0001

Table 5. Standardized coefficients from analysis of individual differences in barks.

Variable	Function 1	Function 2	Function 3	Function 4
Duration	0.438	0.570	0.098	0.438
Bark Harmonic Structure	-0.253	-0.272	-0.916	-0.074
Max dB	-0.643	-0.075	0.487	0.740
Mean	-0.153	0.757	-0.451	0.619
Standard Deviation	-0.536	-0.168	0.602	0.253
Kurtosis	0.598	0.008	-0.125	0.234
HNR	-0.002	-0.121	0.027	0.758

Table 6. Training data classification matrix from analysis of individual differences in barks.

	M-5320	M-5416	M-5429	F-5438	F-5471	Percent Correct
M-5320	49	6	8	3	2	72
M-5416	3	23	2	2	9	59
M-5429	2	2	17	0	0	81
F-5438	4	1	1	11	2	58
F-5471	0	12	1	2	57	79
Total	58	44	29	18	70	72

Table 7. Test data classification matrix from analysis of individual differences in barks.

	M-5320	M-5416	M-5429	F-5438	F-5471	Percent Correct
M-5320	17	0	3	1	2	74
M-5416	2	6	0	1	4	46
M-5429	1	0	4	0	2	57
F-5438	2	1	0	3	1	43
F-5471	0	1	1	1	21	88
Total	22	8	8	6	30	69

Table 8. Howl data for coyotes recorded at the NWRC Logan Field Station, July, 1998.<sup>1</sup>

Variable	F-5414	F-5438	M-5320	M-5416	M-5429	M-5430
Start Frequency (Hz)	394 ± 9.0	446 ± 9.9	380 ± 5.8	392 ± 5.5	370 ± 6.9	374 ± 4.7
End Rise Frequency (Hz)	936 ± 32	1,028 ± 35	1,141 ± 21	1,072 ± 20	673 ± 24	808 ± 17
Maximum Frequency (Hz)	1,026 ± 23	1,089 ± 25	1,326 ± 15	1,213 ± 14	818 ± 17	988 ± 12
Start Fall Frequency (Hz)	978 ± 29	1,001 ± 32	1,172 ± 19	1,116 ± 18	671 ± 22	865 ± 15
End Frequency (Hz)	559 ± 34	646 ± 37	1,023 ± 22	504 ± 21	361 ± 26	480 ± 18
Rise Duration (ms)	241 ± 23	234 ± 25	216 ± 15	262 ± 14	191 ± 17	267 ± 12
End Rise to Max Duration (ms)	442 ± 69	312 ± 76	450 ± 45	318 ± 43	397 ± 53	370 ± 37
Max to Start Fall Duration (ms)	440 ± 105	846 ± 115	989 ± 68	631 ± 64	780 ± 81	376 ± 55
Fall Duration (ms)	68 ± 11	73 ± 12	70 ± 7.3	72 ± 6.9	156 ± 8.6	74 ± 5.9
Rise Slope (Hz/ms)	2.67 ± 0.27	2.69 ± 0.29	4.15 ± 0.17	2.84 ± 0.16	2.16 ± 0.20	1.82 ± 0.14
End Rise to Max Slope (Hz/ms)	0.30 ± 0.08	0.52 ± 0.09	0.53 ± 0.05	0.47 ± 0.05	0.44 ± 0.06	0.57 ± 0.04
Max to Start Fall Slope (Hz/ms)	-0.34 ± 0.08	-0.19 ± 0.09	-0.23 ± 0.05	-0.23 ± 0.05	-0.27 ± 0.06	-0.62 ± 0.04
Fall Slope (Hz/ms)	-6.60 ± 0.58	-5.13 ± 0.64	-2.08 ± 0.38	-10.49 ± 0.36	-2.54 ± 0.45	-5.74 ± 0.31
Rise Nonlinearity	0.48 ± 0.12	0.42 ± 0.13	0.82 ± 0.07	0.51 ± 0.07	0.64 ± 0.09	1.01 ± 0.06
Middle Nonlinearity	0.00 ± 0.00	0.21 ± 0.17	0.00 ± 0.00	0.02 ± 0.09	0.46 ± 0.12	0.92 ± 0.08
Fall Nonlinearity	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.21 ± 0.04	0.11 ± 0.03
50 to 100 Hz Frequency Shifts	0.00 ± 0.00	0.05 ± 0.07	0.00 ± 0.00	0.07 ± 0.04	0.08 ± 0.05	0.12 ± 0.03
100+ Hz Frequency Shifts	0.13 ± 0.11	0.00 ± 0.00	0.18 ± 0.07	0.08 ± 0.07	0.44 ± 0.09	0.23 ± 0.06
0 to 50 Hz Rise Wavers	0.22 ± 0.10	0.00 ± 0.00	0.18 ± 0.07	0.30 ± 0.06	0.13 ± 0.08	0.24 ± 0.05
50 to 100 Hz Rise Wavers	0.09 ± 0.07	0.32 ± 0.07	0.16 ± 0.04	0.08 ± 0.04	0.05 ± 0.05	0.08 ± 0.04
100 to 200 Hz Rise Wavers	0.17 ± 0.06	0.05 ± 0.06	0.09 ± 0.04	0.11 ± 0.04	0.08 ± 0.04	0.04 ± 0.03
200+ Hz Rise Wavers	0.04 ± 0.05	0.16 ± 0.06	0.07 ± 0.03	0.15 ± 0.03	0.00 ± 0.00	0.01 ± 0.03
50 to 100 Hz Middle Wavers	0.17 ± 0.15	0.21 ± 0.17	0.42 ± 0.10	0.10 ± 0.09	0.21 ± 0.12	0.64 ± 0.08
100 to 200 Hz Middle Wavers	0.09 ± 0.12	0.00 ± 0.00	0.04 ± 0.08	0.00 ± 0.00	0.33 ± 0.09	0.48 ± 0.06
200+ Hz Middle Wavers	0.09 ± 0.06	0.00 ± 0.00	0.05 ± 0.04	0.05 ± 0.04	0.08 ± 0.05	0.08 ± 0.03
Body Shape	2.65 ± 0.30	3.37 ± 0.33	3.22 ± 0.20	3.00 ± 0.19	3.38 ± 0.23	2.67 ± 0.16

<sup>1</sup> Values are mean ± standard error. Sample sizes: 23 from F-5414, 19 from F-5438, 55 from M-5320, 61 from M-5416, 39 from M-5429, and 83 from M-5430.

Table 9. Discriminant function statistics from analysis of individual differences in howls.

Function	Eigenvalue	Relative Proportion	Squared Canonical Correlation	X <sup>2</sup> ; DF	p(X <sup>2</sup> )
1	2.8561	0.550	0.7406	588.40, 55	< 0.0001
2	1.4815	0.285	0.5971	320.37, 40	< 0.0001
3	0.6063	0.117	0.3775	139.99, 27	< 0.0001
4	0.1985	0.038	0.1656	45.88, 16	= 0.0001
5	0.0514	0.010	0.0489	9.95, 7	= 0.1913

Table 10. Standardized coefficients from analysis of individual differences in howls.

Variable	Function 1	Function 2	Function 3	Function 4	Function 5
Start Frequency	0.175	0.011	0.246	0.767	0.227
Maximum Frequency	-0.675	-0.293	-0.370	-0.092	0.666
End Frequency	-0.483	0.023	0.010	0.118	-0.594
Fall Duration	-0.189	-0.415	0.407	-0.507	0.156
Rise Slope	-0.375	0.174	0.481	-0.358	-0.365
Maximum to Start Fall Slope	0.095	-0.352	0.430	-0.099	0.131
Fall Slope	-0.256	0.976	0.128	0.129	0.490
Rise Nonlinearity	0.144	0.329	-0.368	-0.244	0.177
50 to 100 Hz Rise Wavers	-0.331	0.089	0.168	0.076	-0.090
100 to 200 Hz Rise Wavers	-0.196	-0.099	0.098	-0.155	-0.733
50 to 100 Hz Middle Wavers	0.010	0.381	-0.425	0.004	-0.050

Table 11. Training data classification matrix from analysis of individual differences in howls.

	M-5320	F-5414	M-5416	M-5429	M-5430	F-5438	Percent Correct
M-5320	32	2	4	0	1	2	78
F-5414	0	9	0	1	4	3	53
M-5416	0	3	37	3	0	2	82
M-5429	0	0	0	26	1	2	90
M-5430	0	7	0	6	48	1	77
F-5438	0	1	0	1	0	12	86
Total	32	22	41	37	54	22	79



Table 12. Test data classification matrix from analysis of individual differences in howls.

	M-5320	F-5414	M-5416	M-5429	M-5430	F-5438	Percent Correct
M-5320	14	0	0	0	0	0	100
F-5414	0	4	0	0	1	1	67
M-5416	0	0	16	0	0	0	100
M-5429	0	0	0	9	1	0	90
M-5430	0	6	0	0	14	1	67
F-5438	0	1	1	0	0	3	60
Total	14	11	17	9	16	5	83

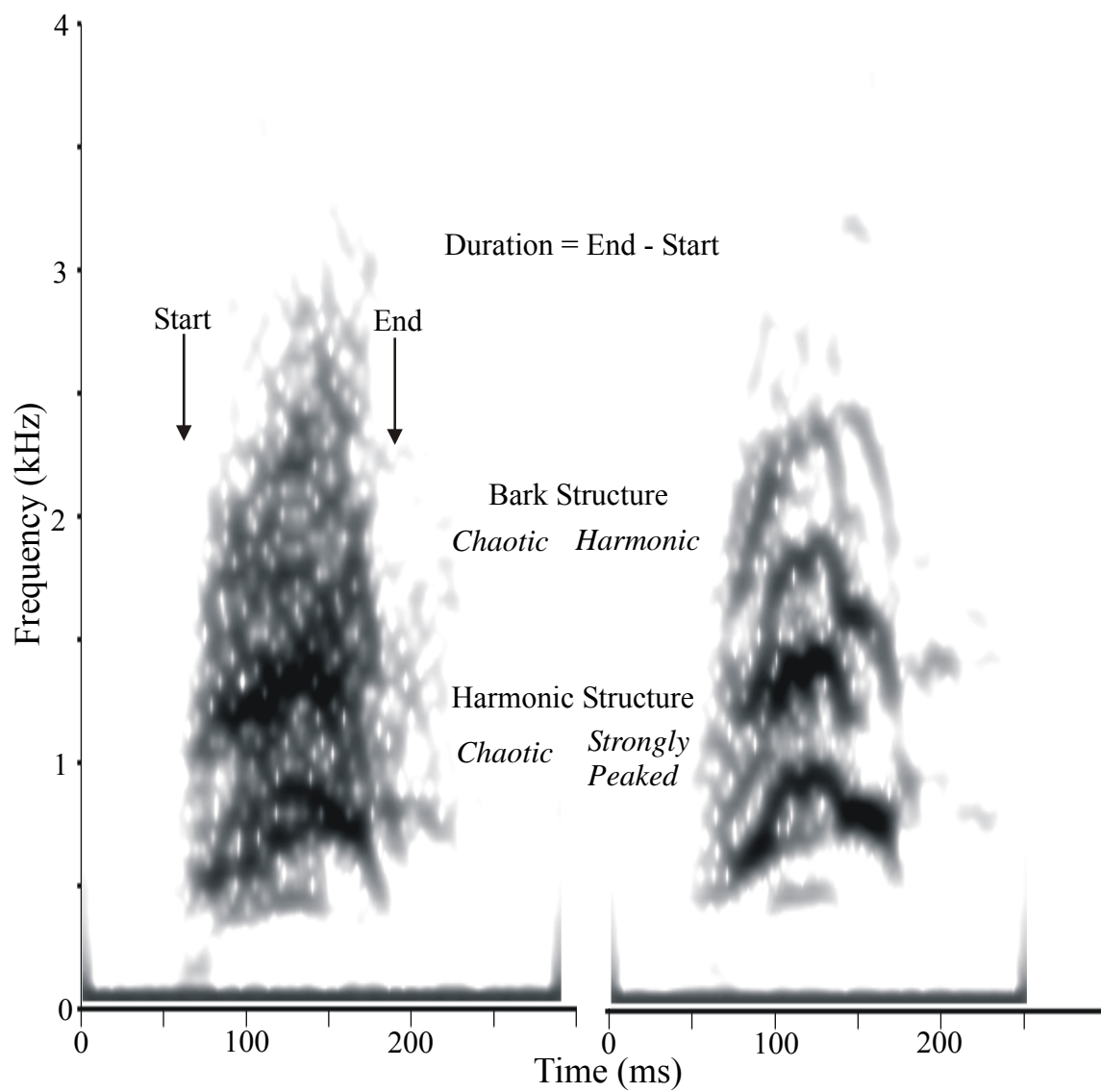


Figure 1. Bark spectrogram measurements and their corresponding variables.

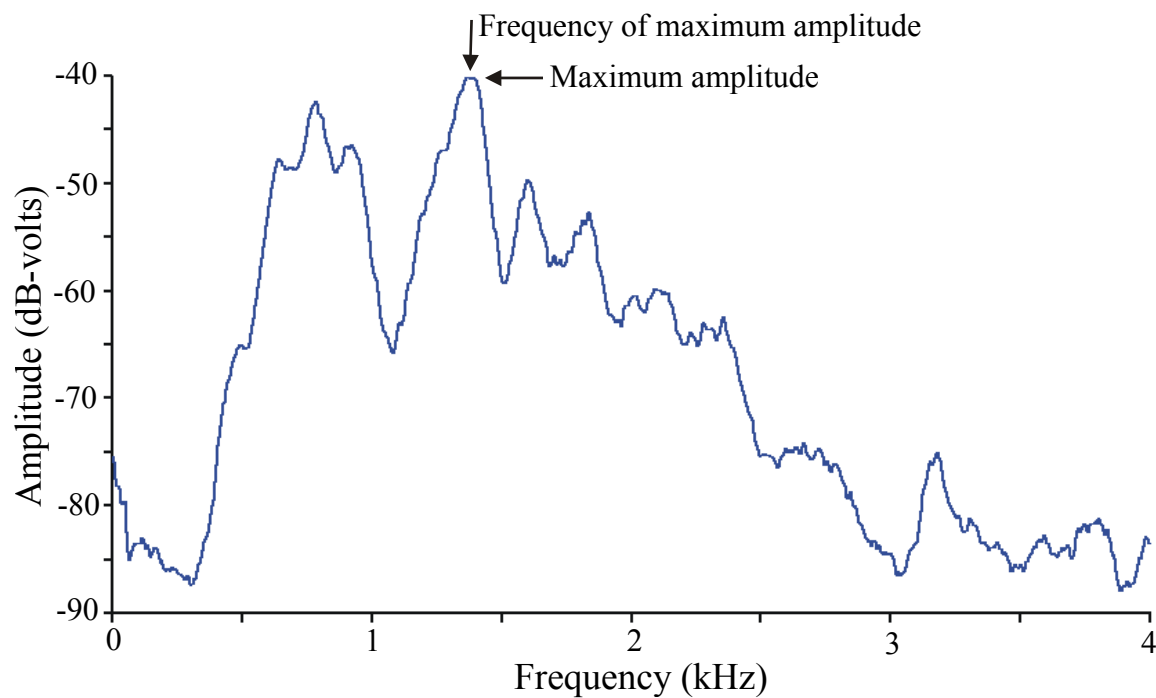


Figure 2. Bark power spectrum variables. Power spectrum is for the right-hand bark from Figure 1.

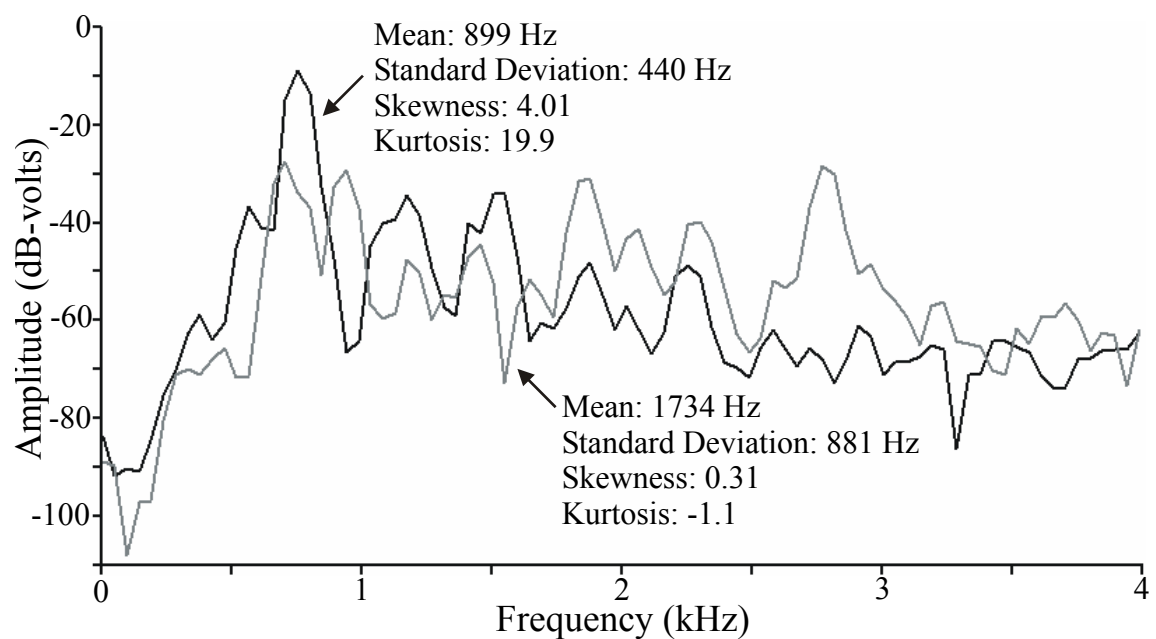


Figure 3. Bark power spectra that illustrate different values for spectral moments.

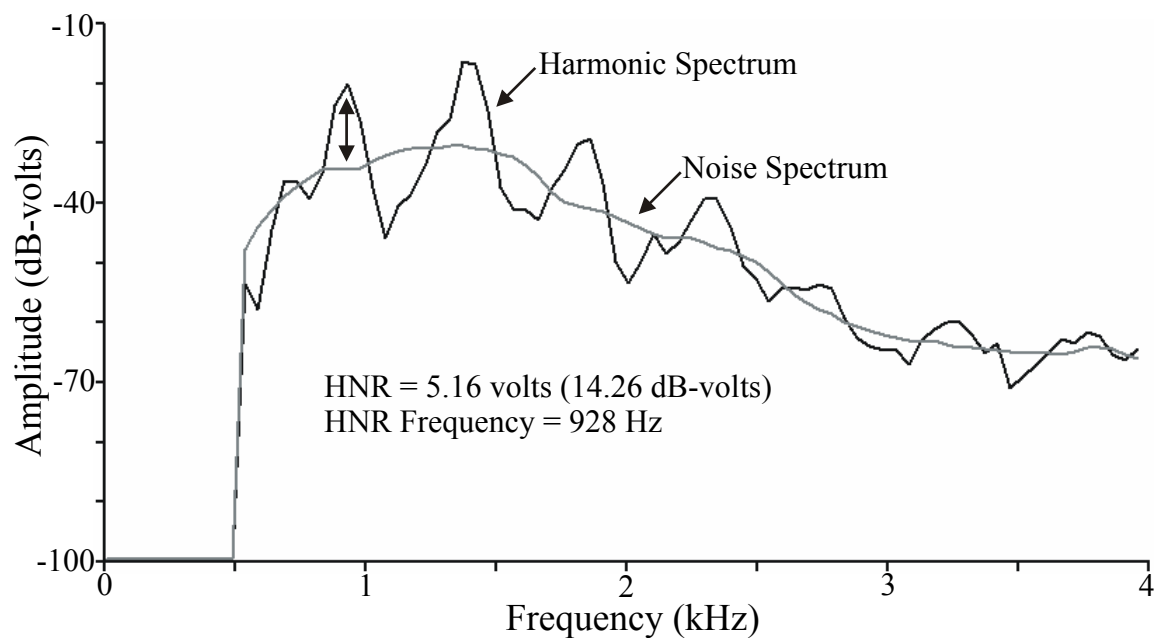


Figure 4. Calculation of the Harmonic-to-Noise Ratio (HNR), using the bark from the right side of Figure 1.

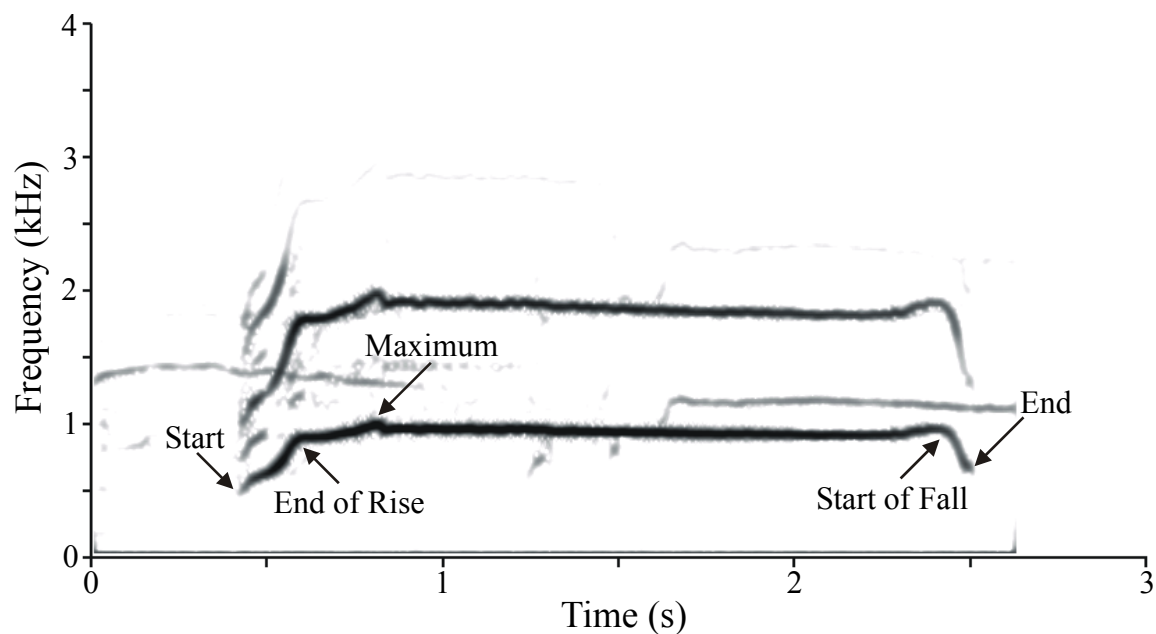


Figure 5. Locations of howl frequency and time measurements.

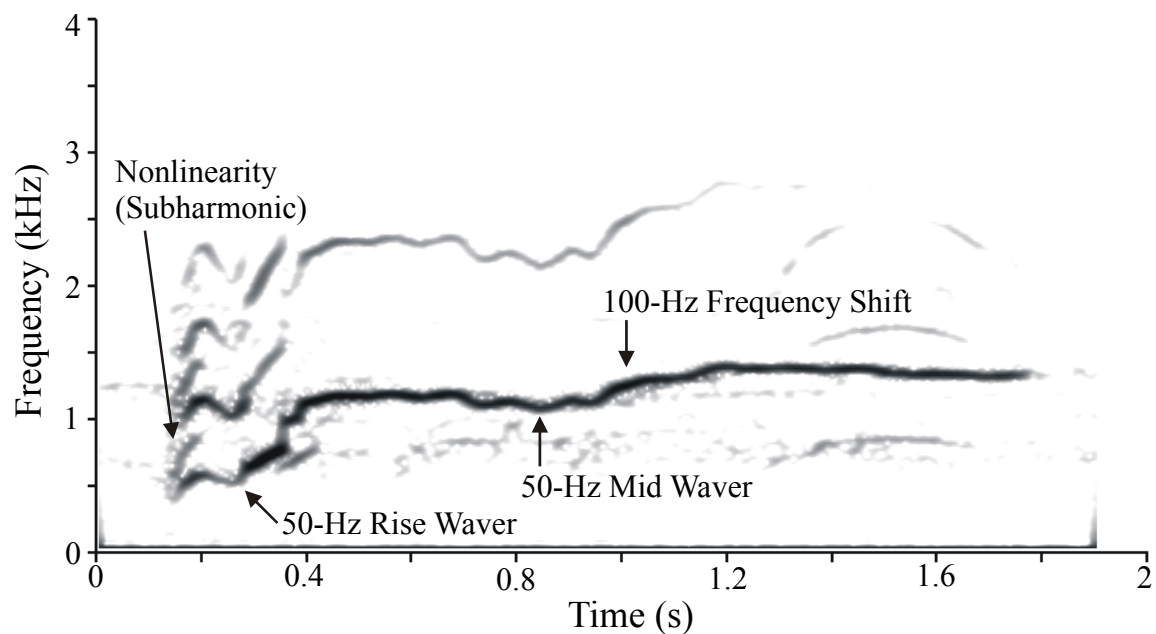


Figure 6. Measurements of howl nonlinearities and frequency modulation.

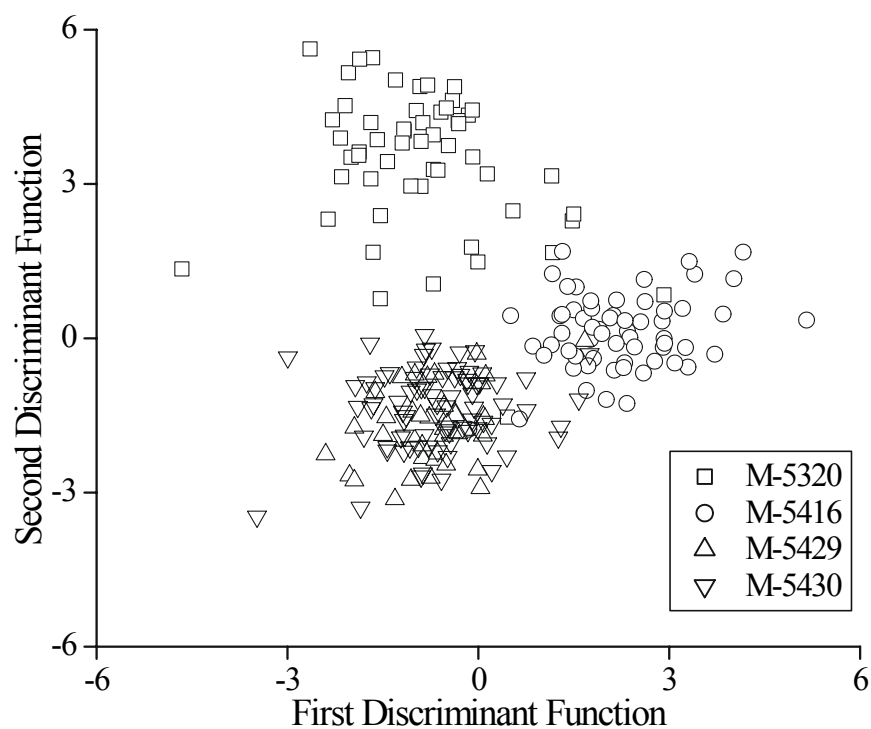


Figure 7. Plot of first two discriminant functions for classifying male howls. Functions were derived from training data and applied to all male howls.

### CHAPTER 3. INFORMATION CONTENT OF COYOTE LONG-RANGE VOCALIZATIONS: TRANSMISSION OF INDIVIDUALLY SPECIFIC VOCAL CUES

**Abstract:** I investigated whether characteristics of coyote barks and howls changed depending on the distance from the sound's source. Recordings of 293 barks and 280 howls from 3 female and 4 male coyotes (4 captive breeding pairs) were obtained and then re-recorded at 10 m, 500 m, and 1,000 m. Vocalization features were measured at each distance and analyzed to determine whether individually distinctive characteristics were stable over biologically relevant distances. Howl characteristics did not degrade with distance, and discriminant analysis was 75% accurate at assigning howls among 6 individuals. Bark characteristics were highly unstable with distance and it is unlikely that barks could be used for individual recognition over long distances. The disparate results for the 2 vocalization types suggest that howls and barks serve separate functions. Howls are optimized to convey information, while barks are more suitable for attracting attention and acoustic ranging.

**Key words:** bark, *Canis latrans*, coyote, discriminant analysis, howl, information, ranging, vocalization.

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Although many studies have searched for vocal features that identify individual animals (Chapter 2), few have tested whether these individually specific characteristics of long-range vocalizations can actually be detected at biologically relevant distances. Instead, most researchers assume that discriminating features carry as far as the sound can be perceived. Elephant vocalizations are a case in point. The infrasonic component

of elephant calls can carry up to 10 km, but useful discrimination does not occur over these distances – elephants typically only recognize individuals that are less than 1.5 km away. This is because elephants recognize individuals based on higher frequency components of vocalizations that degrade much more quickly than infrasound (McComb et al. 2003).

Vocal characteristics that show strong reliability regardless of distance should be preferred by receivers interested in determining the identity of a vocalizing animal (Naguib and Wiley 2001). Recognition based on features that are distance-independent would allow receivers to develop a simple, general purpose perceptual template that could be used for matching vocalizations. If individually specific features of vocalizations degrade or are altered with distance, animals attempting to identify the source of a call would be required to estimate the distance to the source and then factor in a complex understanding of how acoustic features change with distance. Only then would they be able to match the vocalization to a mental template that had been formed by listening to the sender at close range.

If, however, the purpose of a long-distance vocalization is to provide location information to receivers, then characteristics that degrade with distance are actually preferred. Humans and birds have been shown to estimate distance to sounds (often called “ranging”) using 3 separate techniques: amount of reverberation, absolute magnitude, and relative intensity of high-frequency components. Reverberation is rarely present in animal vocalizations; it is created as sounds reflect off of features in the environment. Therefore increased reverberation in a sound, which is manifested as a blurring of sound energy, almost always indicates a greater distance to the source. The

other types of ranging rely on learned knowledge of the amplitude and general characteristics of the sound at its source. Distance estimation based on absolute magnitude takes advantage of the tendency for more distant sounds to have lower amplitudes, while ranging based on relative intensity involves judging the ratio of high to low frequencies in vocalizations. Because high frequencies are attenuated more rapidly than low frequencies, a low ratio indicates a distant sound (Naguib and Wiley 2001).

There is therefore a tradeoff between vocalization characteristics useful for information transfer and qualities useful for ranging. Vocalization types or components used for long-range communication of content should be stable over distances used by the species, while vocalizations used for ranging should degrade relatively quickly. This chapter tests whether individual information in coyote barks and howls is conserved when transmitted over distances up to 1 km. It also addresses the possible presence of characteristics useful for ranging – or distance estimation – and how data processing and the playback speaker altered vocalizations. I predicted that howls would be better suited than barks for conveying individually specific cues over biologically relevant distances, but that barks might be suitable for ranging. I also predicted that sound processing and playback would slightly alter vocalization characteristics.

## **METHODS**

### **Recording and Sound Processing Procedures**

*Initial Recordings and Sound Processing.*--Recording procedures, equipment, and study animals were described in Chapter 2. Recordings were collected at the US Department of Agriculture, Wildlife Services, National Wildlife Research Center (NWRC) field station in Logan, Utah, between 8 July 1998 and 27 July 1998. The initial data set contained 641



single vocalizations (318 barks and 323 howls) from 4 pairs of coyotes. Using Sound Forge 4.5 (Sonic Foundry, Madison, Wisconsin, USA) with Noise Reduction 2.0 (Sonic Foundry, Madison, Wisconsin, USA), research associate Maja Makagon and I removed excessive background noise by isolating a 50 to 250 ms segment of noise preceding each vocalization and iteratively reducing noise between 3 and 5 times. Noise reduction was run with default parameters, and noisier sounds were subjected to more iterations. The vocalizations were all peak-normalized to -0.7 dB, and then compared to copies of the original vocalizations that had only been normalized. We eliminated 56 sounds from use because they sounded distorted, leaving 585 vocalizations (293 barks and 292 howls). I digitally resampled the sounds from 25 kHz to 44.1 kHz using Sound Forge's maximum-accuracy anti-alias filtering and then converted the resulting sounds to stereo. This step was necessary to produce a standard format audio CD that could be read by the CD player in my playback equipment. The playback CD was 50 minutes long, and contained each vocalization separated by 4 seconds of silence. The order of presentation of sounds on the playback was the same order the sounds were recorded; this meant that each pair's vocalizations were present on only 2 or 3 sections of the playback.

*California Playbacks.*--Recordings were played using a timer-controlled playback unit with 3 25-watt Johnny Stewart long-range predator calling speakers (Hunter's Specialties, Cedar Rapids, Iowa, USA) oriented at opposing angles. The speakers were connected to an automobile CD player that was controlled by a timer and powered with a 25 amp-hour battery. Speaker height was 50 cm, and microphone height was 1.2 m for all recordings. The playback device was set in open annual grassland at the Gray Davis Dye Creek Preserve (DCP), in Tehama County, northern California. The DCP had been

the site of extensive playback experiments with coyotes over the previous 2 years. The specific playback site was selected with the help of GIS software to be isolated and flat; elevation decreased only 6 meters between the playback site and the location of the 1-km recording site. During each recording session, we used duplicate sets of recording equipment to record at 2 distances. Sunrise was approximately 0630, and we recorded near this time because wind speed was minimal. On 23 August 2002 we recorded at 10 m and 1,000 m from source, beginning at 0650; on 24 August we recorded at 500 m and 2,000 m, beginning at 0610; and on 30 August we recorded at 1,000 m and 1,500 m, beginning at 0610.

*Final Sound Processing.*--The new recordings were digitized with a 25-kHz sample rate using RTSD 1.1 (Engineering Design, Belmont, Massachusetts, USA) and a 50 kHz Dart Digital Signal Processor card (Engineering Design, Belmont, Massachusetts, USA). Maja Makagon isolated all vocalizations from the 10-m and 500-m recordings. She also isolated vocalizations from the 2 1,000-m recordings; the 23 August recording was used unless recording quality was poor and the 30 August recording was better, which was the case for 261 vocalizations. The 1,500-m and 2,000-m recordings were not processed because they had long poor quality sections.

An additional 12 howls were excluded from analysis after this point. Ten howls were excluded because they were made by individuals who each contributed less than 15 vocalizations. One sound was removed because it contained a loud background vocalization that interfered with measurements, and another was eliminated because its spectrogram characteristics were severely altered by noise reduction.

The final vocalization library therefore contained 293 barks and 280 howls at each of 5 different processing and physical distances from the original vocalizations: raw or initial recordings, noise reduced and normalized sounds, 10-m recording, 500-m recording, and 1,000-m recording.

### **Bark Measurements and Variables**

Bark variables were described in Chapter 2. The random number for each bark (used to determine which barks were in the discriminant analysis training sets) was the same across the distance data sets.

After analyzing the bark data, I discovered some unexpected patterns in how some bark variables changed with distance (e.g. Figure 8, where the average bark structure for 2 animals showed a strong dip at 500 m). I thought the patterns might be explained by recording quality, so I calculated a Signal-to-Noise Ratio (SNR) to compare the amplitude of bark spectral energy to low frequency noise (from wind and small aircraft). SNR was calculated using a program written for Signal 4.0 (Engineering Design, Belmont, Massachusetts, USA). My SNR program determined the time of peak amplitude by bandpass filtering 12-kHz sounds to remove energy below 300 Hz and above 4 kHz, found the time of maximum amplitude, and selected an 82-ms segment from the original 25-kHz sound that was centered at this time of peak energy. A 2-k FFT was computed, and smoothed with a 50-Hz moving average. On the resulting power spectrum, I recorded the maximum value between 50 and 300 Hz (the noise measurement) and the maximum value between 500 and 3,000 Hz (the signal measurement). SNR was the signal minus the noise (Figure 9).

## Howl Measurements and Variables

Howl variables were described in Chapter 2, and each howl had the same random number assigned to it at each distance. All howl measurements were made on spectrograms produced in Signal 3.1 from 25-kHz audio files. Spectrograms were displayed using a 5-ms step between successive FFTs and a 1,024-point FFT size, were zoomed to approximately 1 second by 1 kHz for measurement, and had measurement resolutions of at least 1.7 ms and 5.0 Hz.

*Time and Frequency Measurement Issues.*--Time and frequency measurements were taken at 5 points along the fundamental for each howl: the howl's start, the end of the howl's rising portion, the point of maximum frequency, the start of the howl's falling portion, and the end of the howl (Chapter 2, Figure 5). If 1 of these points was not visible on the fundamental, which was only an issue for some howls recorded at 500 m and 1,000 m, then the point was measured on the lowest usable harmonic (almost always the first harmonic) and the frequency measurement was divided to yield the equivalent fundamental measurement. Maja Makagon measured each howl in the order it was originally recorded, and she measured all howls for 1 distance before moving on to howls at a different distance.

When I subsequently compared the spectrograms and measurements for individual howls at different distances, I discovered that even though the spectrograms for the howls were practically identical, the measurements fluctuated considerably (e.g. the end of the rise in Figure 10). Perhaps the greatest contribution to this measurement error involved magnification of minor decisions about where to measure the howls. For example, the "end of the rise" and "start of the fall" of a howl are arbitrary points along a

continuously changing curve, and small changes in exactly how an observer measured these points led to large differences in the actual measurements. Another contributing factor to measurement error was measuring howls on different harmonics at different distances. Even though the frequency measurements on a harmonic are an exact multiple of the fundamental frequency, the harmonics will appear to start before and extend beyond the fundamental when they have more sound energy than the fundamental. A final cause of measurement error stemmed from the noise reduction algorithm used to clean up vocalizations for playback. If the pattern of background noise changed over the course of a sound (as when a background vocalization decreased in intensity or changed frequency), noise reduction removed sound energy from the portion of the howl where the background energy was originally present. This produced a characteristic frequency gap or intensity reduction in the spectrogram (Figure 11). For a given howl, there might have been a complete frequency gap in the noise reduced and 10-m recording, and then an intensity reduction at the 500-m and 1,000-m distances. Frequency gaps led to errors when measurements were taken only above the gap, which ignored orphaned vocalization segments that were present below the gap.

I remedied these measurement errors by intensively reviewing the data. For each howl, if any measurement deviated beyond a threshold value from the average measurement, I sequentially viewed the howl at each distance and remeasured the appropriate frequency-time pairs. The threshold value depended on the measurement being checked because there was more spectrogram variability in some measurements than others. For example, the beginning and end of a howl often had low sound intensity, so measurements of the start and end point naturally fluctuated at different distances.

Maximum frequency, on the other hand, showed practically no variation with distance. I used the following threshold values when checking the data: start and end frequency could deviate up to 50 Hz from the average (and up to 125 Hz for measurements taken on the raw vocalizations), the frequencies for the end of the rise or start of the fall could deviate up to 15 Hz, the maximum frequency was allowed to deviate up to 10 Hz, and the durations of the 2 middle sections were allowed to deviate up to 40 ms. Roughly 65% of the measurements exceeded at least 1 threshold and needed to be checked.

By measuring all 5 processing and physical distances of a howl at nearly the same time, I minimized the effect of small shifts in measurement location, eliminated the effect of measuring on different harmonics, and removed the effect of variations introduced by noise reduction (Figure 10). Making measurements in this way allowed me to look for subtle distance-related effects, such as frequency shifting and time compression or expansion, without swamping these effects in measurement error.

### **Statistical Analyses**

*Discriminant Analyses.*--I used linear discriminant analysis to examine whether bark and howl variables could be used to tell individuals apart at different distances. Procedures were identical to those described in Chapter 2. The 6 discriminant analyses from Chapter 2 were repeated at each of the other 4 distances (noise reduced and normalized, 10-m, 500-m, and 1,000-m) to determine whether classification accuracy changed with distance.

I assessed the relative importance of different variables at different distances using covariance-controlled partial F-ratios. The partial F-ratio for a variable represented the discriminating power of that variable after the contributions of all other variables in the model were removed. The magnitude of the statistic therefore ranks the importance

of the variable in the analysis, and an F-test can be used to determine if the variable contributes statistically significant discriminatory power (McGarigal et al. 2000). Although the F-ratios were not strictly comparable between models, it was still useful to examine how relative rankings and ratio magnitudes changed for different models. The F-ratios were equivalent to the F-to-remove statistic used to select variables for discriminant models. Because I set my critical value for variable selection at  $\alpha$  equals 0.15 to decrease the chance of a Type II error (i.e. the probability of excluding an important variable), some variables were included in the models that were not significant at an  $\alpha$  of 0.05.

Repeating the discriminant analyses using recordings made at different distances was useful for determining whether individually and sexually specific information was present at the different distances. But this technique did not address the constancy of information relative to distance or potential distortion of sound characteristics due to playback. Variables that did not change between 10 m and 1,000 m were potentially much more useful for discriminating sex or individual identity, because they allowed for a stable model that functioned equally well at any distance.

*MANOVA Procedures.*--I used repeated measures MANOVA to investigate how bark and howl variables changed with distance. All MANOVAs were calculated using JMP IN 4.0 (SAS Institute, Cary, North Carolina, USA), with individual as the model effect and the measurements of a variable over distance as the repeated measure. This model structure allowed me to investigate whether measurements differed by individual, whether measurements differed over distance, and whether individual and distance interacted. I matched the output from the MANOVAs with graphs of individual means at the different

distances to qualitatively assess patterns of differences indicated by the statistical results. As with discriminant analysis, MANOVA is robust to violations of the assumptions of multivariate normality and equal covariance matrices, especially if the sample size is large (Zar 1999:320-1).

The MANOVA results were used to generate a list of variables for incorporation into a distance-independent discriminant analysis. Variables were selected if the F-ratio for an individual effect was more than double the F-ratio for the distance effect, which indicated that individual differences outweighed any differences due to distance. Variables were also selected if the F-test for a distance effect was non-significant given a Bonferroni-corrected alpha of  $0.05/n$ , where  $n$  equaled the number of bark or howl variables tested. This selection procedure ensured that variables with biologically important distance effects were excluded from further consideration. The shortened list of variables was used in accordance with the previously described methods to generate a discriminant model based on the 10-m training data. The resulting discriminant functions were then checked against the 10-m, 500-m, and 1,000-m test data.

## **RESULTS**

### **Bark Analyses**

Mean bark measurements changed dramatically with distance (Table 3). The only exception was bark duration, which was stable at the 3 re-recorded distances. The partial F-ratios were consistent for the discriminant analyses classifying barks among the 5 individuals (Table 14). Bark duration was one of the most important variables in all the models, and was usually closely followed by bark harmonic structure (reflecting the presence and shape of the harmonics). Mean, skewness, and kurtosis all had low to



moderate importance, while harmonic-to-noise ratio (HNR), HNR frequency, and bark structure either had low importance or were not included in the models. Maximum dB level was generally important, except for the 10-m distance, and the usefulness of standard deviation and the frequency of maximum dB level fluctuated.

The classification accuracy was higher for initial and noise-reduced models than for the other 3 distances (Table 15). The first 2 models had kappas around 60%, while the other 3 models had chance-corrected accuracies near 45%. The female-only (Table 16) and male-only (Table 17) models had relatively high raw classification accuracies that belied the low chance-corrected accuracies for the test data. The male-based models had moderate kappas with large confidence intervals, and the female models had generally low kappas and extremely large confidence intervals. In fact, the 10-m female-only model had a confidence interval that encompassed 0, indicating a model accuracy that did not statistically differ from chance.

The repeated measures MANOVAs of bark variables showed significant individual, distance, and interaction effects for all variables, except that duration lacked an interaction effect (Table 18). In every case, the distance effect was approximately equal to or larger than the individual effect, indicating that the effect of distance on the variables matched or exceeded any differences due to the individuals. I did not attempt to use discriminant analysis to classify barks at different distances using the same model – the highly significant distance effects and relative weakness of individual effects would have precluded accurate classifications.

The presence of strong interaction effects in the bark MANOVAs was unexpected. The potential causes of the interactions and the likely explanations for the

distance effects are detailed in Appendix 3. Briefly, the interaction effects stemmed from 4 sources: 1) various types of measurement error affected bark structure, bark harmonic structure, mean, and HNR; 2) sample size effects combined with skewed data distributions influenced maximum dB frequency and HNR frequency measurements; 3) nonlinear effects created by the playback equipment created interacting effects for higher order spectral moments; and 4) the increased influence of atmospheric effects at greater distances affected maximum dB measurements. Recording quality (signal-to-noise ratio [SNR] measurements) did not contribute to the interaction effects.

Most of the distance effects stemmed from a combination of sound processing (i.e. noise reduction and amplitude normalization), the characteristics of the playback speaker, and attenuation of sound with increasing distance. In particular, the playback equipment strongly overemphasized high frequencies and increased bark durations.

### **Howl Analyses**

The howl data differed markedly from the bark data in that means for most variables were stable over distance (Table 8). The exceptions to this rule were start and end frequencies, and correspondingly the start and end durations and slopes. These variables changed as the low amplitude and frequency starts and ends of howls were degraded with distance and masked by low frequency background noise. Nonlinearities and wavers in the rising portion of the howl also tended to disappear with distance; the nonlinearities were more likely to be lost in background noise at greater distances, and wavers tended to fade when they occurred in the low-amplitude beginning of a howl.

*Discriminating Individuals at Different Distances.*--Partial F-ratios were consistent across distances for the models built to discriminate between the 6 individuals (Table 20). The

maximum frequency and fall slope were always the most important variables. The start frequency, maximum to start fall slope, and the number of 50-Hz to 100-Hz wavers in the middle of the howl were always somewhat important, while the end frequency, number of 50-Hz to 100-Hz rise wavers and number of 100-Hz to 200-Hz rise wavers were consistently included in the models with fairly low rankings. Rise slope, fall duration, and rise nonlinearities were somewhat important in the initial model, but their importance declined with increasing distance. This was not surprising, considering that nonlinear phenomena were harder to detect at greater distances, and that measures associated with the start and end frequency tended to degrade as low amplitude and low frequency information was lost at longer distances. The end rise to maximum and maximum to start fall durations appeared in more distant models; these variables based on the howl middle section may have partially compensated for the loss of information contained in the rise slope, fall duration, and number of rise nonlinearities.

The summary statistics for the discriminant models based on all 6 individuals were consistently good (Table 21). The squared canonical correlation for the first discriminant function was always between 0.74 and 0.76, so individual identity explained three quarters of the variability in this function. The test data accuracy was always greater than the training accuracy, which varied between 76% and 81%, with corresponding kappa estimates of 70% to 76%.

The models classifying the 4 males consistently performed even better than the model with all individuals (Table 22), perhaps because of larger average sample sizes per individual. The male-only squared canonical correlation ranged from 0.78 to 0.80, and

again the test data were always classified more accurately than the training data.

Training accuracy ranged between 85% and 88%, and kappa was between 0.80 and 0.84.

In contrast, the female-based models performed poorly (Table 23). The squared canonical correlations were much lower (between 0.47 and 0.58), and the test data were always classified less accurately than the training data. Raw classification accuracy of the test data ranged from 64% to 82%, but kappa estimates indicated that 4 of the models were not statistically better than chance. The failure of these models was likely due to the low sample size for the female-based models, which used 31 howls for training and 11 howls for testing.

*MANOVA Results.*--The repeated measures MANOVA results for the 26 howl variables showed considerably fewer distance and interaction effects (Table 24) than the comparable results for bark measurements. Sixteen variables had no distance or interaction effects, indicating that distance did not affect any potential individual differences. Six of these 16 variables did indeed have significant individual effects: slope and duration from the maximum to start fall, irregularities in the middle and fall, and middle wavers from 50-Hz to 100-Hz and 100-Hz to 200-Hz.

Of the 10 variables with significant distance or interaction effects, 5 had distance effect F-ratios that were less than half the individual effect F-ratios. In these cases I felt that individual effects outweighed any potential distance effects enough that discriminant analysis would still be stable. Indeed, the individual means for the end of rise, maximum, and start of fall frequencies showed no obvious change over distance despite highly significant distance effects (Figure 12). The rise and fall slope means did show some

slight interaction and distance effects, but individual differences were clearly much stronger (Figure 13).

The remaining 5 variables – start and end frequency, rise and fall duration, and the number of rise nonlinearities – were excluded from the distance-independent discriminant analysis. All of these variables showed significant distance effects with magnitudes similar to or greater than the individual effects. I predicted that removal of these 5 variables would reduce the overall accuracy of the discriminant analysis, but ensure that the models remained relevant at different distances. Start frequency and rise irregularities were moderately useful for individual discrimination, but negative impacts of their loss would probably be limited by the retention of more important variables.

*Distance-Independent Discriminant Analyses.*--Individual discrimination accuracy was slightly reduced in the distance-independent model, but this model was still very successful: approximately 75% of test howls were correctly classified, regardless of the distance (Table 25). This corresponded to a chance-corrected accuracy estimate between 68% and 71%. As usual, the model classifying the 4 males performed even better than the model for all 6 individuals; in this case over 85% of test howls were assigned to the correct male, and kappa estimates exceeded 80% at all test distances. Low sample sizes prevented the female-only model from performing well; kappa estimates fluctuated considerably and confidence intervals were large.

## **DISCUSSION**

### **Effects of Sound Processing and Playback**

One goal of this study was to evaluate the effect of sound processing and playback on recorded vocalizations. Noise reduction and the playback speaker

diminished low amplitude information, which produced noticeable increases in the start and end frequencies, decreases in rise and fall durations, a slight decrease in the number of rise wavers, and variable effects on the slope of the rise and fall. Other low amplitude features, such as howl nonlinearities, were also somewhat diminished by sound processing and playback. Howls were additionally altered by playback in a few ways that were not reflected in the measurements. The speaker introduced frequency reflections when background noise was close to a howl's fundamental frequency. The playback equipment also overemphasized high frequency components of vocalizations, as evidenced by harmonics that were stronger in 10-m recordings than in noise-reduced and normalized howls (Figure 14).

Bark measurements were strongly affected by noise reduction and the playback speaker because many bark variables were related to the frequency distribution of sound energy. Noise reduction removed background noise and apparently favored lower frequencies, which led to increased HNR, bark structure, and bark harmonic structure measurements and decreased values for the spectral moments. The playback equipment then overemphasized high frequency components and introduced some noise. This led to decreased HNR, bark structure, and bark harmonic structure; increased means and standard deviations; and convergent higher order moments. Playback also increased bark duration, possibly by adding reverberation to the barks. In general, the effects of noise reduction and playback were partially compensatory. However, bark means were elevated above the range of initial bark means, bark durations were elevated into the high end of initial bark durations, and skewness, kurtosis, and HNR were decreased to the lower end of the values seen for the original bark recordings (Appendix 3).

The overall effect of my sound processing and playback procedures was to introduce occasional acoustic artifacts, lose low amplitude information, and overemphasize high frequency sound energy. These alterations to the original coyote vocalizations provided listeners with cues that they could use to determine that playbacks were not live animals. However, the frequency reflection artifacts were rare, generally had relatively low amplitude, and were masked by background noise and attenuation at greater distances. The artifact visible in Figure 14 was barely detectable at 500-m and 1,000-m. Similarly, the missing low amplitude information was expected to disappear with increasing distance due to attenuation and background noise.

The high frequency bias was more problematic. High frequency sound is attenuated more rapidly than low frequency sound; the relationship between frequency and attenuation is an approximate function of frequency<sup>1.3</sup> (Pye and Langbauer 1998). So the high frequency energy of barks (at about 2.5 kHz) will attenuate about 8 times faster than the low frequency energy (at around 0.5 kHz). While this means that the speaker's bias should be partially compensated by distance effects, the averages for bark mean frequency showed that values at 500-m and 1,000-m were still generally higher than the original values (**Error! Reference source not found.**). Because many animals use the presence of high frequency sound or the ratio of high- to low-frequency sound to estimate the distance to vocalizing conspecifics (Naguib and Wiley 2001), there is a distinct possibility that the speaker's frequency bias would make playbacks sound artificial to coyotes, or cause them to underestimate the distance to a playback.

### **Barks are Suitable for Distance Estimation**

Chapter 2 documented the presence of information in coyote barks that was useful for identifying individuals. However, barks do not stably convey this information over any appreciable distance. The relative importance of most bark variables shifted in different analyses, plus none of the variables (except duration) showed any stability in their means as distance increased. The features of barks changed too dramatically to allow for the use of a distance-independent discriminant analysis to classify individuals.

Barks appear to be unsuitable for stable information transmission, but they are appropriate for a few other purposes, including acoustic ranging. Barks are short, noisy vocalizations that cover a broad frequency range – from below 500 Hz to over 2.5 kHz. This type of sound has some distinct advantages when used in the context of agonistic interactions or as an alarm call. Barks are likely to trigger the acoustic-startle reflex in nearby animals, which causes them to increase their alertness and orient towards the sound source (Owren and Rendall 2001). This would be a useful response for a coyote that is challenging a conspecific or trying to alert his or her pack of danger.

Barks are also well structured for use in distance assessment. Broadband noisy vocalizations are ideal for determination of distance via relative intensity changes, and the frequency range of barks is only slightly lower than the 1-kHz to 4-kHz range needed for maximum sound transmission distance in most environments (Wiley and Richards 1978). The abrupt nature of barks, with their sudden onset and offset, also makes these vocalizations suitable for ranging based on reverberation (Naguib and Wiley 2001). Although ranging has never been experimentally demonstrated in canids, I expect that coyotes are adept at locating barking individuals.



### **Howls Reliably Transmit Information**

Howls are structurally different from barks; they are tonal, relatively long, frequency modulated vocalizations with a dominant frequency near 1 kHz. Wiley and Richards (1978) predicted that optimal information transmission over long distances would be obtained by tonal, frequency modulated vocalizations with frequencies between 1 kHz and 4 kHz. Howls therefore meet the criteria for an optimum information-containing long-distance vocalization. Despite marked intra-individual variability, each coyote used a particular combination of howl features in a specific way, which allowed the howls to be correctly classified to the vocalizing animal 80% of the time. When a few variables that showed distance effects were excluded, a discriminant model based on vocalizations recorded at 10-m classified test howls recorded at 10-m, 500-m, and 1,000-m with 75% accuracy – regardless of distance.

Howls contain individually specific cues that are transmitted to distances of at least 1,000-m without any noticeable degradation of information content. Howls conceivably also contain information about the sex of the howling individual (Appendix 1), plus howls may include more detailed information about the signaler's emotional and physical status. This sort of information does not need to be conveyed in a consistent manner by all coyotes; in fact there might be adaptive significance to altering howls in an individually specific way. Theberge and Falls (1967) noted that information in howls could be universal (i.e. species-specific) or individual. Individual information would only be understandable by coyotes familiar with the vocalizing animal. A territory intruder would understand the agonistic threat when an alpha male howled at him, yet

only the alpha male's mate would understand that the extra wavering in his howl indicated that he had just killed a large prey item.

Howls can therefore serve typical species-wide functions while also serving as a coded system for familiar animals to communicate privately. This individual communication does not require that individuals hash out a private language; it only requires that coyotes alter their vocalizations in idiosyncratic but consistent ways depending on context, and that close companions are able to associate the context with the altered vocalization. Proving that howls do indeed function in this way would require extensive recordings of familiar animals made in multiple contexts, plus some clever playback experiments.

### **Improving Playback Methods**

My findings suggest some steps that can be taken to improve the realism of playbacks used for behavioral ecology research and coyote management. Barks and howls likely serve complementary purposes; the acoustic structure of barks is well suited to ranging, while howls are better suited to transmitting information over long distances. Coyote vocal bouts almost universally feature both calls, indicating that the overall bout may help conspecifics locate and identify the signaler, as well as judge his or her emotional state based on whether barks or howls predominate. Additionally, coyotes probably recognize individuals and possibly sex based on howl features, and they may respond differently to known animals. If multiple individuals are included on a playback, coyotes may be able to judge how many were involved.

Realistic playbacks should therefore incorporate barks and howls so that study animals receive the complementary information they contain, and should employ

speakers with minimal frequency bias between 250 Hz and 4 kHz so that ranging information is not altered. Playbacks that exclude 1 type of vocalization or the other could be used to test this complementarity, but care should be taken because these playbacks will be confounded by the differing emotional intensities conveyed by barks and howls. Realistic playbacks should also include vocalizations from only 1 or a few individuals, and the experimental design should incorporate the possibility of different responses based on the number, sex, and familiarity of individuals used for the playback. Playback experiments that account for and test the likely information content of coyote long-range vocalizations will aid the development of selective coyote control methods and bring us much closer to understanding the communication system of this wily canid.

Table 13. Bark data at 5 different distances for coyotes recorded at the NWRC Logan Field Station and re-recorded at the Dye Creek Preserve.<sup>1</sup>

Variable	Initial	NR & Norm	10 meters	500 meters	1,000 meters
Duration (ms)	122 ± 1	119 ± 1	134 ± 1	135 ± 1	132 ± 1
Bark Structure	1.81 ± 0.04	1.99 ± 0.04	1.96 ± 0.05	1.72 ± 0.04	1.75 ± 0.04
Bark Harmonic Structure	2.68 ± 0.08	2.78 ± 0.07	2.62 ± 0.08	2.14 ± 0.07	2.20 ± 0.07
Max dB (dB-volts)	-43.8 ± 0.3	-21.7 ± 0.2	-41.0 ± 0.1	-51.0 ± 0.3	-54.3 ± 0.4
Max dB Frequency (Hz)	780 ± 15	781 ± 15	993 ± 23	899 ± 21	1,009 ± 23
Mean (kHz)	1,244 ± 9	1,152 ± 10	1,492 ± 5	1,275 ± 8	1,299 ± 8
Standard Deviation (Hz)	655 ± 5	520 ± 5	679 ± 4	609 ± 3	591 ± 6
Skewness	1.53 ± 0.03	1.24 ± 0.04	0.98 ± 0.01	1.25 ± 0.02	1.03 ± 0.03
Kurtosis	3.30 ± 0.14	2.76 ± 0.20	1.46 ± 0.06	2.59 ± 0.09	2.54 ± 0.10
HNR (volts)	7.82 ± 0.25	9.02 ± 0.28	6.56 ± 0.25	6.92 ± 0.22	5.34 ± 0.17
HNR Frequency (Hz)	739 ± 17	770 ± 25	744 ± 16	824 ± 25	957 ± 31

<sup>1</sup> Values are mean ± standard error for 293 barks from 5 coyotes.

Table 14. Partial F-ratios of variables in models discriminating barks by individual.<sup>1</sup>

Variable	Initial	NR & Norm	10 meters	500 meters	1,000 meters
Duration	17.32	11.61	17.57	12.01	10.65
Bark Harmonic Structure	9.92	9.37	14.57	5.19	6.09
Max dB	7.45	17.38	--	14.57	8.80
Max dB Frequency	--	--	6.57	--	5.97
Mean	4.34	2.72	2.99	3.55	6.26
Standard Deviation	5.15	25.43	8.66	3.84	3.30
Skewness <sup>2</sup>	N/A	N/A	6.99	5.00	4.19
Kurtosis	4.03	2.09	6.06	3.21	2.84
HNR	2.54	3.57	3.35	--	--
HNR Frequency	--	--	--	--	2.74

<sup>1</sup> Ratios greater than 2.85 are statistically significant at  $\alpha$  of 0.05.

<sup>2</sup> Skewness was excluded from Initial and NR & Norm analyses because of correlations with other variables that exceeded 0.9.

Table 15. Summary statistics for models discriminating barks by individual.

Distance	Squared Canonical Correlation	Training Accuracy (Percent)	Test Accuracy (Percent)	Training Kappa <sup>†</sup>	Test Kappa <sup>†</sup>
Initial	0.653	72	69	0.63 ± 0.08	0.58 ± 0.14
NR & Norm	0.665	77	70	0.69 ± 0.07	0.61 ± 0.14
10 meters	0.406	66	58	0.56 ± 0.08	0.44 ± 0.15
500 meters	0.311	59	58	0.47 ± 0.08	0.46 ± 0.14
1,000 meters	0.498	66	57	0.55 ± 0.08	0.43 ± 0.15

<sup>†</sup> Estimate ± 95% confidence interval.

Table 16. Summary statistics for models discriminating barks by individual female.

Distance	Squared Canonical Correlation	Training Accuracy (Percent)	Test Accuracy (Percent)	Training Kappa <sup>†</sup>	Test Kappa <sup>†</sup>
Initial	0.764	97	87	0.91 ± 0.10	0.59 ± 0.38
NR & Norm	0.703	97	90	0.90 ± 0.11	0.71 ± 0.31
10 meters	0.543	89	74	0.69 ± 0.18	0.33 ± 0.40
500 meters	0.379	81	77	0.48 ± 0.22	0.44 ± 0.37
1,000 meters	0.667	96	90	0.88 ± 0.12	0.74 ± 0.28

<sup>†</sup> Estimate ± 95% confidence interval.

Table 17. Summary statistics for models discriminating barks by individual male.

Distance	Squared Canonical Correlation	Training Accuracy (Percent)	Test Accuracy (Percent)	Training Kappa <sup>†</sup>	Test Kappa <sup>†</sup>
Initial	0.507	79	72	0.67 ± 0.11	0.53 ± 0.22
NR & Norm	0.589	82	77	0.71 ± 0.11	0.62 ± 0.21
10 meters	0.466	77	72	0.63 ± 0.12	0.53 ± 0.23
500 meters	0.411	72	70	0.55 ± 0.12	0.52 ± 0.22
1,000 meters	0.491	76	70	0.62 ± 0.12	0.56 ± 0.21

<sup>†</sup> Estimate ± 95% confidence interval.

Table 18. Repeated measures MANOVA results for bark variables.

Variable	Individual		Distance		Interaction	
	$F_{4, 288}$	$p(F)^1$	$F_{4, 285}$	$p(F)^1$	$F^2_{16, 1152}$	$p(F)^1$
Duration	31.2	< 0.0001	86.9	< 0.0001	1.73	0.0362
Bark Structure	18.6	< 0.0001	18.6	< 0.0001	3.90	< 0.0001
Bark Harmonic Structure	22.4	< 0.0001	20.8	< 0.0001	3.31	< 0.0001
Max dB	15.5	< 0.0001	4,749.4	< 0.0001	18.21	< 0.0001
Max dB Frequency	26.1	< 0.0001	36.9	< 0.0001	4.20	< 0.0001
Mean	40.3	< 0.0001	926.4	< 0.0001	12.50	< 0.0001
Standard Deviation	17.8	< 0.0001	294.0	< 0.0001	13.01	< 0.0001
Skewness	29.0	< 0.0001	148.2	< 0.0001	15.98	< 0.0001
Kurtosis	28.6	< 0.0001	59.5	< 0.0001	14.28	< 0.0001
HNR	16.7	< 0.0001	51.4	< 0.0001	5.44	< 0.0001
HNR Frequency	12.2	< 0.0001	21.5	< 0.0001	3.92	< 0.0001

<sup>1</sup>  $\alpha$  equals 0.0045<sup>2</sup> F-test is Pillai's Trace

Table 19. Howl data at 5 different distances for coyotes recorded at the NWRC Logan

Field Station and re-recorded at the Dye Creek Preserve.<sup>1</sup>

Variable	Initial	NR & Norm	10 meters	500 meters	1,000 meters
Start Frequency (Hz)	385 ± 3	439 ± 3	484 ± 3	495 ± 3	506 ± 3
End Rise Frequency (Hz)	938 ± 13	937 ± 13	939 ± 13	938 ± 13	939 ± 13
Maximum Frequency (Hz)	1,090 ± 12	1,090 ± 12	1,092 ± 12	1,092 ± 12	1,093 ± 12
Start Fall Frequency (Hz)	972 ± 13	972 ± 13	974 ± 13	974 ± 13	974 ± 13
End Frequency (Hz)	593 ± 16	657 ± 16	655 ± 16	665 ± 16	671 ± 15
Rise Duration (ms)	241 ± 7	215 ± 6	191 ± 6	186 ± 6	180 ± 6
End Rise to Max Duration (ms)	380 ± 20	380 ± 20	379 ± 20	380 ± 20	380 ± 20
Max to Start Fall Duration (ms)	645 ± 33	646 ± 33	645 ± 33	645 ± 33	645 ± 33
Fall Duration (ms)	84 ± 4	72 ± 3	73 ± 4	71 ± 3	70 ± 3
Rise Slope (Hz/ms)	2.68 ± 0.09	2.69 ± 0.09	2.76 ± 0.10	2.72 ± 0.09	2.80 ± 0.10
End Rise to Max Slope (Hz/ms)	0.50 ± 0.02	0.51 ± 0.02	0.51 ± 0.02	0.52 ± 0.02	0.51 ± 0.02
Max to Start Fall Slope (Hz/ms)	-0.36 ± 0.03	-0.35 ± 0.03	-0.36 ± 0.03	-0.36 ± 0.03	-0.36 ± 0.03
Fall Slope (Hz/ms)	-5.64 ± 0.24	-5.36 ± 0.23	-5.35 ± 0.23	-5.43 ± 0.25	-5.28 ± 0.23
Rise Nonlinearity	0.73 ± 0.04	0.55 ± 0.04	0.55 ± 0.04	0.49 ± 0.04	0.44 ± 0.03
Middle Nonlinearity	0.35 ± 0.05	0.35 ± 0.05	0.32 ± 0.05	0.27 ± 0.04	0.31 ± 0.05
Fall Nonlinearity	0.06 ± 0.01	0.05 ± 0.01	0.04 ± 0.01	0.04 ± 0.01	0.05 ± 0.01
50 to 100 Hz Frequency Shifts	0.06 ± 0.02	0.06 ± 0.02	0.06 ± 0.02	0.06 ± 0.02	0.06 ± 0.02
100+ Hz Frequency Shifts	0.19 ± 0.03	0.19 ± 0.03	0.19 ± 0.03	0.19 ± 0.03	0.19 ± 0.03
0 to 50 Hz Rise Wavers	0.21 ± 0.03	0.20 ± 0.03	0.18 ± 0.03	0.17 ± 0.03	0.16 ± 0.02
50 to 100 Hz Rise Wavers	0.11 ± 0.02	0.10 ± 0.02	0.09 ± 0.02	0.09 ± 0.02	0.10 ± 0.02
100 to 200 Hz Rise Wavers	0.08 ± 0.02	0.08 ± 0.02	0.08 ± 0.02	0.08 ± 0.02	0.08 ± 0.02
200+ Hz Rise Wavers	0.06 ± 0.01	0.06 ± 0.01	0.06 ± 0.01	0.06 ± 0.01	0.06 ± 0.01
50 to 100 Hz Middle Wavers	0.35 ± 0.04	0.34 ± 0.04	0.34 ± 0.04	0.33 ± 0.04	0.34 ± 0.04
100 to 200 Hz Middle Wavers	0.20 ± 0.04	0.21 ± 0.04	0.21 ± 0.04	0.22 ± 0.04	0.21 ± 0.04
200+ Hz Middle Wavers	0.06 ± 0.02	0.06 ± 0.02	0.06 ± 0.02	0.06 ± 0.02	0.06 ± 0.02
Body Shape	3.00 ± 0.09	3.00 ± 0.09	3.01 ± 0.09	3.01 ± 0.09	2.98 ± 0.09

<sup>1</sup> Values are mean ± standard error for 280 howls from 6 coyotes.

Table 20. Partial F-ratios of variables in models discriminating howls by individual.

Ratios greater than 2.63 are statistically significant at  $\alpha$  of 0.05

Variable	Initial	NR & Norm	10 meters	500 meters	1,000 meters
Start Frequency	5.34	6.18	5.16	7.62	5.29
Maximum Frequency	13.53	14.40	49.54	14.39	13.78
End Frequency	3.53	2.16	--	2.85	4.89
End Rise to Max Duration	--	--	2.64	2.93	3.08
Max to Start Fall Duration	--	--	3.52	4.35	3.10
Fall Duration	5.36	3.21	4.85	2.37	--
Rise Slope	8.12	7.42	5.45	5.97	3.74
Maximum to Start Fall Slope	6.09	5.16	3.94	4.40	4.39
Fall Slope	13.89	18.45	37.59	10.98	10.75
Rise Nonlinearity	6.17	4.35	3.63	3.55	2.47
Middle Nonlinearity <sup>1</sup>	N/A	--	3.47	N/A	2.96
Fall Nonlinearity <sup>1</sup>	N/A	N/A	N/A	N/A	N/A
50 to 100 Hz Freq Shifts <sup>1</sup>	N/A	N/A	N/A	N/A	N/A
100+ Hz Frequency Shifts	--	--	2.46	--	--
50 to 100 Hz Rise Wavers	3.42	3.46	4.05	4.08	4.00
100 to 200 Hz Rise Wavers	2.54	3.09	2.60	2.82	2.22
50 to 100 Hz Middle Wavers	6.40	5.73	4.64	5.51	3.57
100 to 200 Hz Middle Wavers <sup>1</sup>	N/A	N/A	N/A	N/A	N/A

<sup>1</sup> Fall Nonlinearity, 50 to 100 Hz Frequency Shifts, and 100 to 200 Hz Middle Wavers excluded from analysis because multiple individuals had no variability for these variables. Middle Nonlinearity was excluded from two analyses for the same reason.

Table 21. Summary statistics for models discriminating howls by individual.

Distance	Squared Canonical Correlation	Training Accuracy (Percent)	Test Accuracy (Percent)	Training Kappa <sup>1</sup>	Test Kappa <sup>1</sup>
Initial	0.741	79	83	0.74 ± 0.07	0.79 ± 0.11
NR & Norm	0.738	80	86	0.76 ± 0.07	0.83 ± 0.10
10 meters	0.769	81	85	0.76 ± 0.07	0.81 ± 0.10
500 meters	0.738	76	78	0.70 ± 0.07	0.73 ± 0.12
1,000 meters	0.759	78	81	0.73 ± 0.07	0.76 ± 0.11

<sup>1</sup> Estimate ± 95% confidence interval.

Table 22. Summary statistics for models discriminating howls by individual male.

Distance	Squared Canonical Correlation	Training Accuracy (Percent)	Test Accuracy (Percent)	Training Kappa <sup>1</sup>	Test Kappa <sup>1</sup>
Initial	0.792	87	92	0.82 ± 0.07	0.89 ± 0.09
NR & Norm	0.776	87	90	0.82 ± 0.07	0.87 ± 0.10
10 meters	0.796	88	90	0.84 ± 0.06	0.87 ± 0.10
500 meters	0.775	85	87	0.80 ± 0.07	0.82 ± 0.11
1,000 meters	0.782	87	90	0.82 ± 0.07	0.87 ± 0.10

<sup>1</sup> Estimate ± 95% confidence interval.

Table 23. Summary statistics for models discriminating howls by individual female.

Distance	Squared Canonical Correlation	Training Accuracy (Percent)	Test Accuracy (Percent)	Training Kappa <sup>1</sup>	Test Kappa <sup>1</sup>
Initial	0.522	87	82	0.74 ± 0.24	0.62 ± 0.48
NR & Norm	0.489	77	64	0.55 ± 0.30	0.29 ± 0.55
10 meters	0.581	90	64	0.81 ± 0.21	0.29 ± 0.55
500 meters	0.471	81	64	0.61 ± 0.28	0.27 ± 0.57
1,000 meters	0.518	84	73	0.67 ± 0.26	0.46 ± 0.52

<sup>1</sup> Estimate ± 95% confidence interval.



Table 24. Repeated measures MANOVA results for howl variables.

Variable	Individual		Distance		Interaction	
	$F_{5, 275}$	$p(F)^1$	$F_{4, 271}$	$p(F)^1$	$F^2_{20, 1096}$	$p(F)^1$
Start Frequency	14.63	< 0.0001	376.23	< 0.0001	5.17	< 0.0001
End Rise Frequency	66.09	< 0.0001	8.07	< 0.0001	1.22	0.2246
Maximum Frequency	132.97	< 0.0001	46.55	< 0.0001	2.52	0.0002
Start Fall Frequency	81.40	< 0.0001	9.76	< 0.0001	1.44	0.0928
End Frequency	104.91	< 0.0001	64.33	< 0.0001	5.39	< 0.0001
Rise Duration	3.80	< 0.0024	57.06	< 0.0001	4.98	< 0.0001
End Rise to Max Duration	1.27	0.2793	0.96	0.4315	0.75	0.7782
Max to Start Fall Duration	11.98	< 0.0001	1.98	0.0980	1.37	0.1299
Fall Duration	13.42	< 0.0001	19.50	< 0.0001	3.95	< 0.0001
Rise Slope	20.34	< 0.0001	3.18	0.0141	2.65	0.0001
End Rise to Max Slope	1.98	0.0813	1.00	0.4093	1.47	0.0815
Max to Start Fall Slope	9.37	< 0.0001	0.79	0.5311	0.66	0.8704
Fall Slope	58.59	< 0.0001	7.55	< 0.0001	3.16	< 0.0001
Rise Nonlinearity	9.63	< 0.0001	13.86	< 0.0001	1.13	0.3153
Middle Nonlinearity	16.21	< 0.0001	2.06	0.0861	1.92	0.0085
Fall Nonlinearity	5.22	< 0.0001	1.26	0.2877	0.78	0.7356
50 to 100 Hz Frequency Shifts	1.46	0.2026	0.00	1.0000	0.00	1.0000
100+ Hz Frequency Shifts	2.80	0.0175	0.00	1.0000	0.00	1.0000
0 to 50 Hz Rise Wavers	1.30	0.2632	2.01	0.0938	1.15	0.2929
50 to 100 Hz Rise Wavers	3.39	0.0055	1.94	0.1045	1.21	0.2363
100 to 200 Hz Rise Wavers	1.31	0.2616	0.41	0.8036	0.51	0.9642
200+ Hz Rise Wavers	3.43	0.0051	0.00	1.0000	0.00	1.0000
50 to 100 Hz Middle Wavers	5.55	< 0.0001	0.55	0.7009	0.72	0.8135
100 to 200 Hz Middle Wavers	7.72	< 0.0001	0.47	0.7606	0.63	0.8951
200+ Hz Middle Wavers	0.37	0.8697	0.19	0.9452	0.11	1.0000
Body Shape	2.16	0.0592	1.98	0.0985	1.58	0.0499

<sup>1</sup>  $\alpha = 0.0019$ <sup>2</sup> F-test is Pillai's Trace

Table 25. Summary statistics for distance-independent discriminant models.

Model	Squared Canonical Corr.	Percentage Correct				Kappa <sup>1</sup>			
		10 m Train	10 m Test	500 m Test	1 km Test	10 m Train	10 m Test	500 m Test	1 km Test
Indiv.	0.756	80	76	75	74	0.75 ± 0.07	0.71 ± 0.12	0.69 ± 0.12	0.68 ± 0.12
Females	0.532	81	73	82	91	0.62 ± 0.27	0.46 ± 0.52	0.63 ± 0.46	0.81 ± 0.35
Males	0.884	85	89	87	89	0.79 ± 0.07	0.85 ± 0.11	0.82 ± 0.11	0.85 ± 0.11

<sup>1</sup> Estimate ± 95% confidence interval.

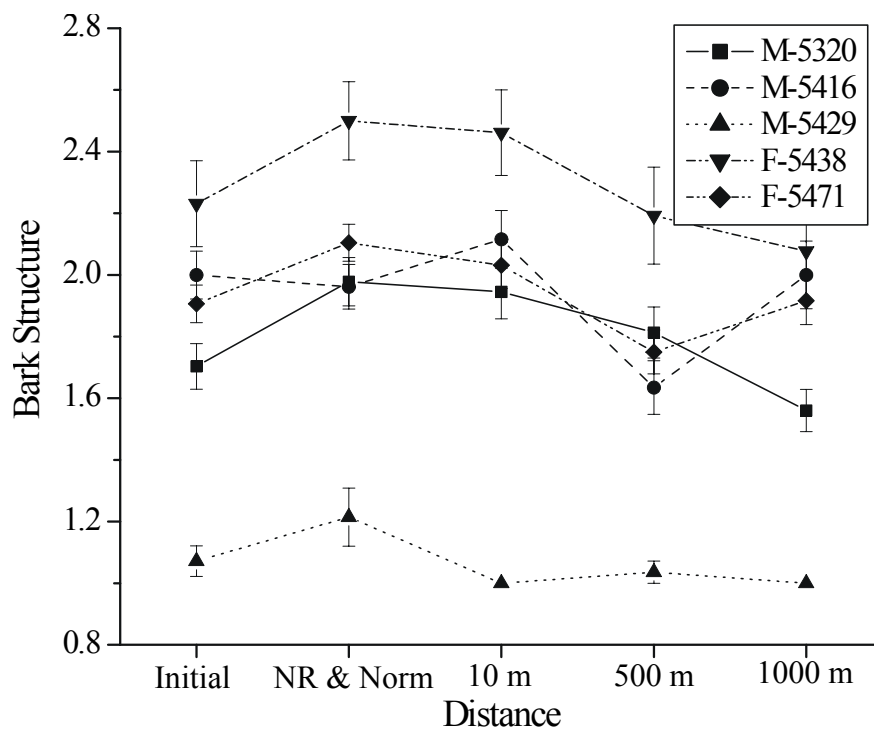


Figure 8. Bark structure: mean and standard error for each individual at each distance.

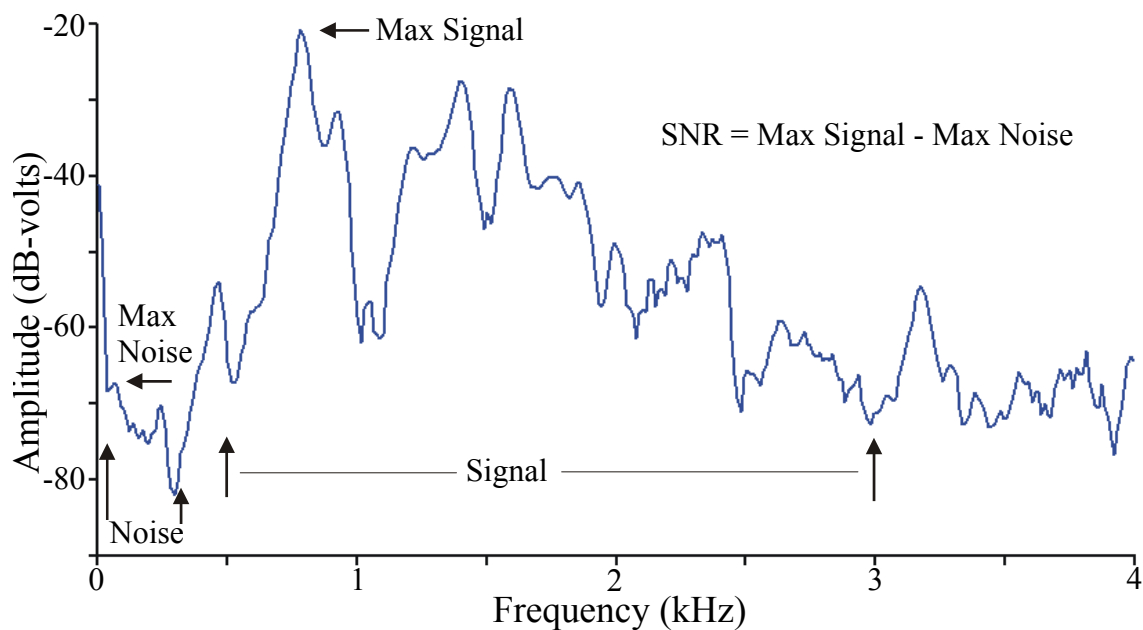


Figure 9. Signal-to-Noise Ratio (SNR) calculation.

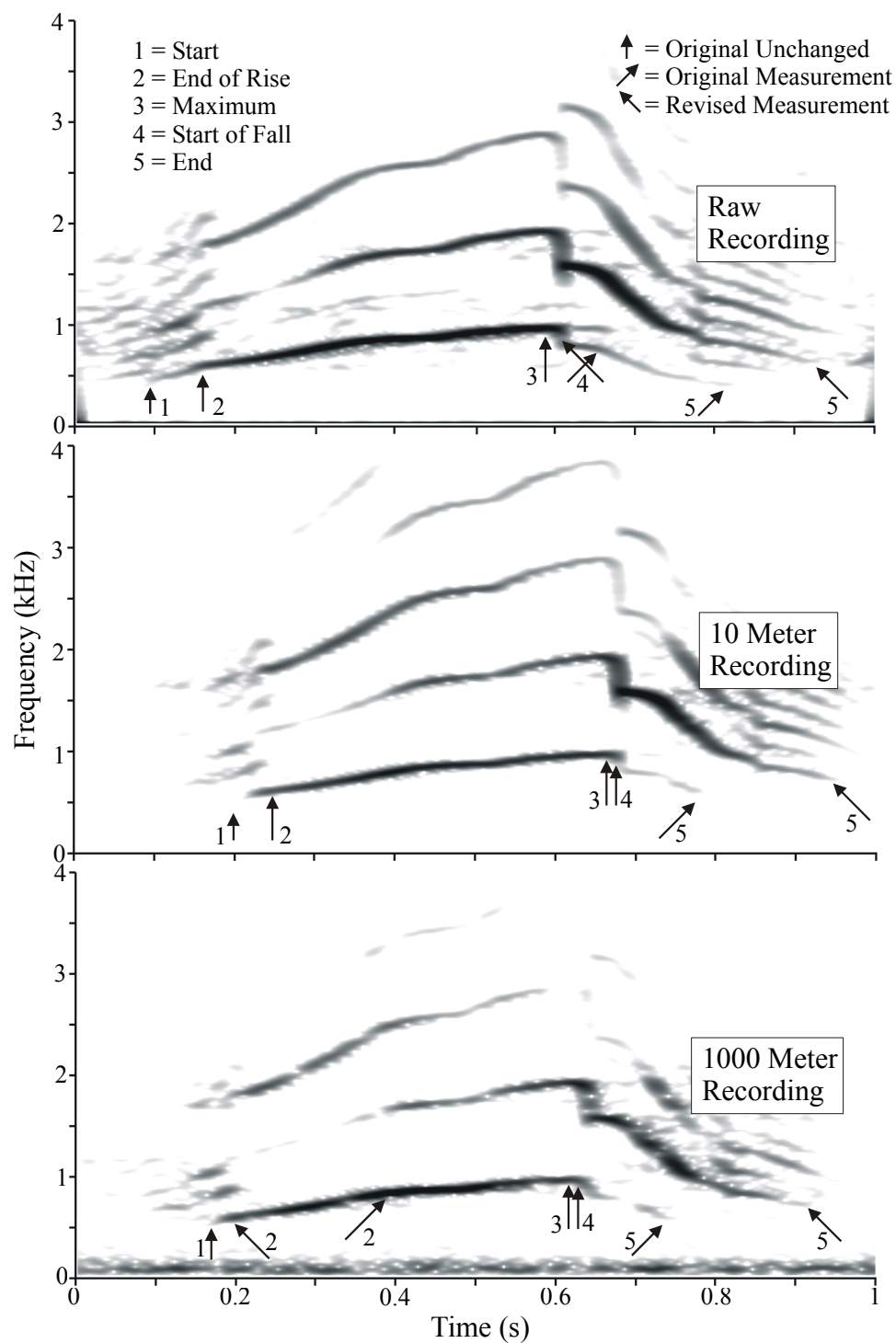


Figure 10. Howl spectrograms for three distances, illustrating measurement difficulties.

Revised measurements corrected inconsistencies in location of start of rise and start of fall, and use the stronger first harmonic for measuring the howl's end.

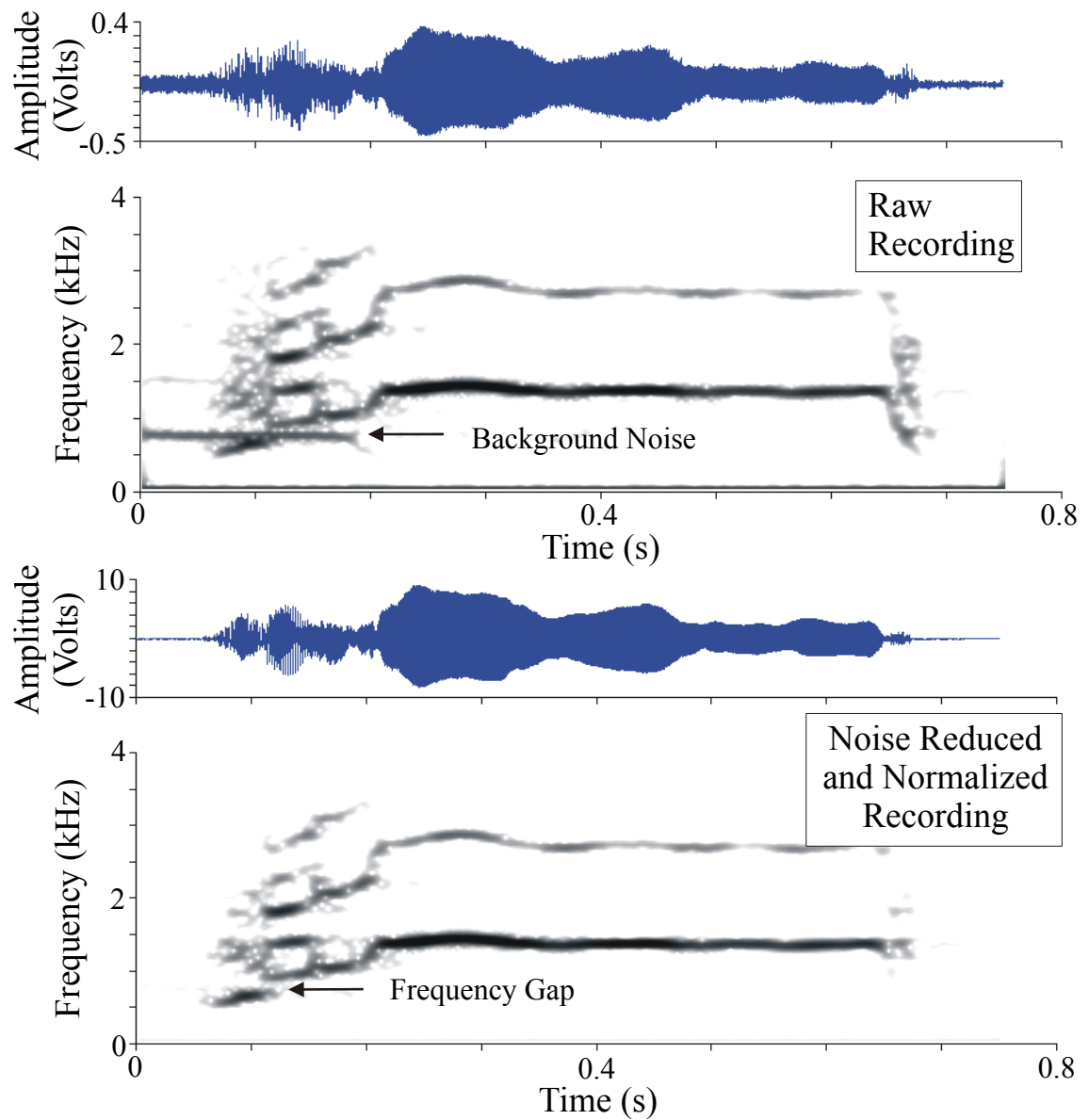


Figure 11. Spectrograms illustrating an occasional problem with noise reduction.

Background noise that slowly decreases in frequency in the raw vocalization (top) results in a frequency gap in the noise reduced and normalized vocalization (bottom).

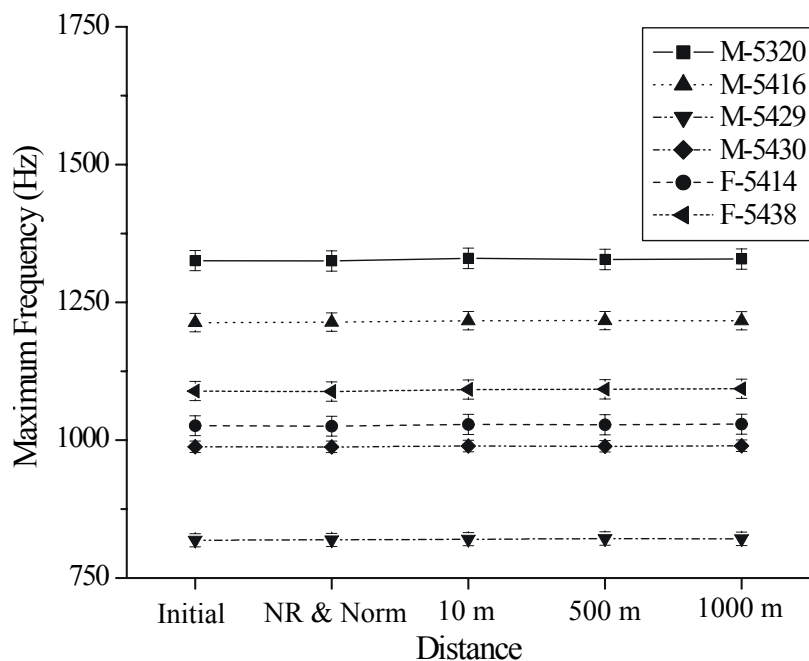


Figure 12. Howl maximum frequency: mean and standard error for each individual at each distance. End of rise and start of fall frequencies show a similar pattern.

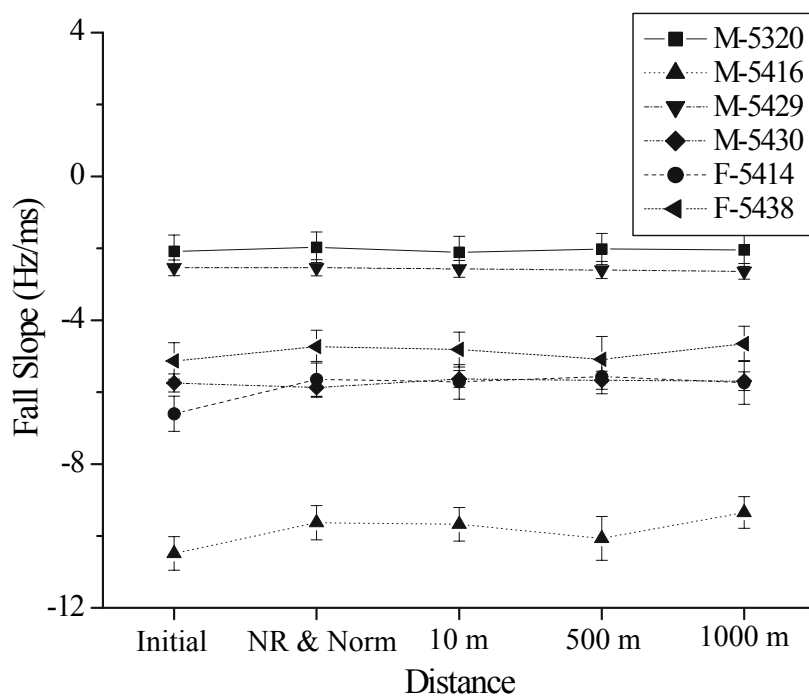


Figure 13. Howl fall slope: mean and standard error for each individual at each distance.

Rise slope shows a similar pattern.

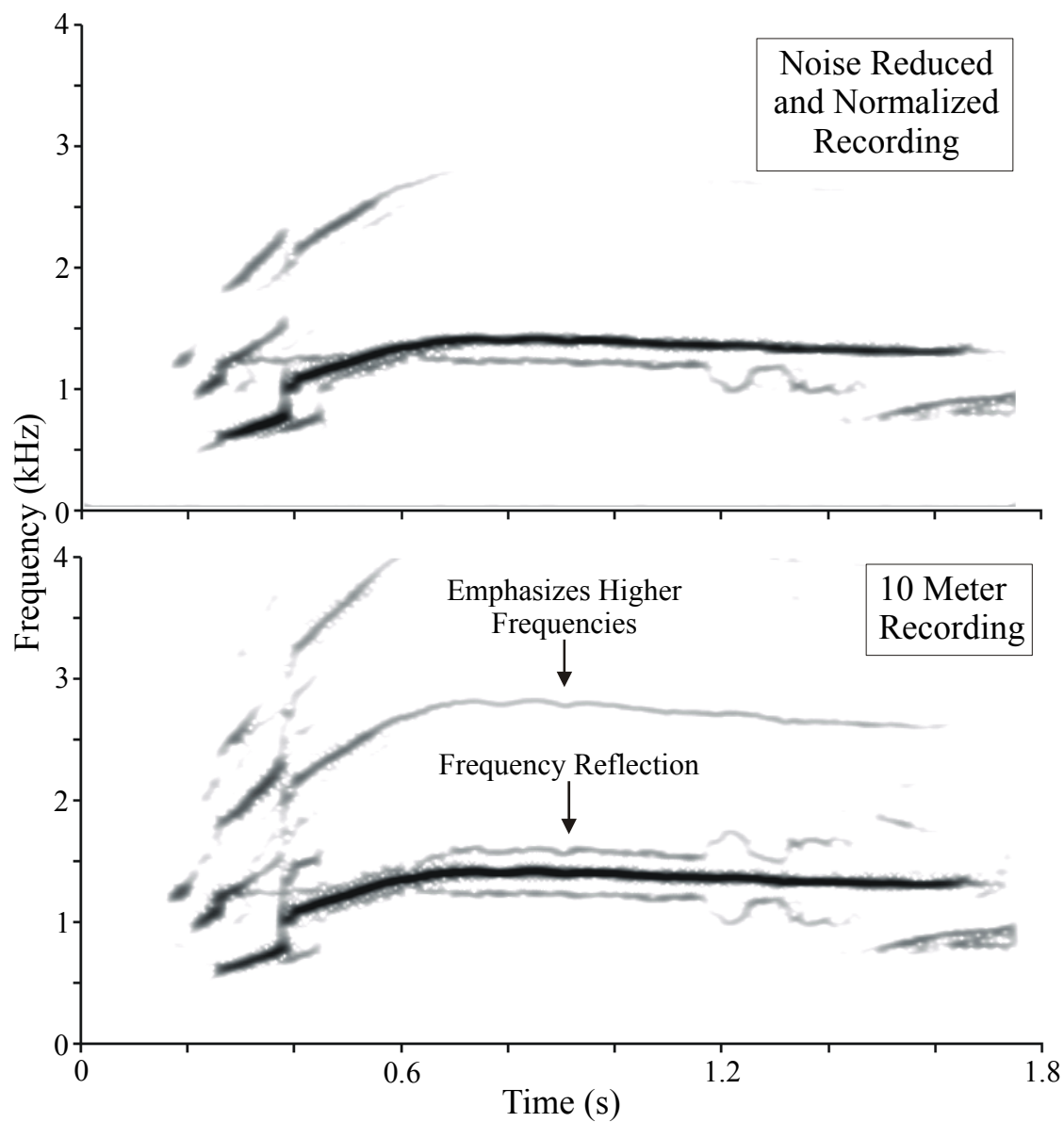


Figure 14. Effects of playback speaker on howl spectrograms.

## CHAPTER 4. THE POTENTIAL UTILITY OF AUDIO PLAYBACK FOR SELECTIVE COYOTE CONTROL

**Abstract:** Coyotes involved in livestock depredation are usually territorial dominant (alpha) individuals, but many coyote control methods are not selective towards this social class. Techniques that incorporate coyote calling – principally “calling and shooting” and “denning” – show some potential for being effective because calling can simulate an intruder and attract the ire of dominant coyotes. This study used a radio collared coyote population on the Gray Davis Dye Creek Preserve in northern California. I applied a multivariate information-theoretic approach to the investigation of factors affecting coyote vocal and approach responses to a variety of playback stimuli. Transients almost never vocally responded to playbacks, and territorial coyotes (alphas and betas) were much more likely to respond to group coyote vocalizations than to a silent control, siren, solo coyote vocalizations, or human imitations of coyotes and prey. Males vocally responded more than females, and responses were slightly higher before sunrise when the moon was up and bright. During these conditions, estimated vocal response rates to group vocalizations were over 55% for territorial males, 42% for alpha females, 11% for beta females, and below 4% for transients. Territorial coyotes were twice as likely to approach playbacks as transients, and coyotes more readily approached playbacks of group howls than the other playback types. Approach rates were highest during the breeding and whelping seasons (1 January to 15 June), when playbacks were within the responding coyote’s home range, when playbacks took place at or before sunrise, and when there were no spontaneous coyote vocalizations preceding playback. When conditions were optimal, alphas were estimated to approach 47% of the time and betas

approached 49% of the time; transients had only a 27% approach rate. These results demonstrate the potential to selectively kill specific problem coyotes using targeted control that employs coyote calling. However, it is important to verify this research through an operational test that compares the selectivity and efficacy of calling techniques with other control methods.

**Key words:** Approach response, *Canis latrans*, coyote, curiosity, depredation management, playback study, social status, territory defense, vocal response.

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### **Coyote Depredation Management**

Coyotes are blamed for approximately \$40 million in livestock losses every year (Chapter 1). These losses are not spread evenly among producers; 10% of sheep ranchers lose more than 20% of their lambs each year (Wagner 1988:29-36). Livestock producers typically have narrow profit margins, so operations that sustain heavy losses must implement coyote control to stay in business. Nonlethal methods are the first line of defense against coyote damage. Some of these methods, which include the use of guard animals, improved fencing, and shed lambing, effectively reduce coyote predation in certain situations (Chapter 1). However, none of these techniques are 100% effective, so there is a need for lethal options that can successfully target problem animals when nonlethal approaches fail.

Problem coyotes are most often territorial dominant (alpha) individuals. Field studies at the University of California's Hopland Research and Extension Center (HREC) documented that alphas whose territories overlapped sheep pastures were more likely to kill livestock than territorial associates (betas), transients, and other alphas (Sacks et al.



1999b, Blejwas et al. 2002). Nonselective coyote removal with traps, snares, and cyanide ejectors (M-44's) was not an effective method of reducing livestock losses at HREC (Conner et al. 1998), probably because the dominant sheep-killing coyotes were relatively impervious to these methods (Sacks et al. 1999a). In contrast, selective removal of specific problem animals resulted in marked decreases in sheep losses for several months; killing did not resume until the surviving breeder found a new mate or a new breeding pair occupied and secured the territory (Blejwas et al. 2002).

Selective lethal control is unfortunately hindered by a paucity of effective, economical, and socially acceptable techniques. Livestock Protection Collars (poison-filled devices that kill coyotes when they attack collared animals) are highly selective and effective, but they are expensive and unacceptable to the general public. The remaining selective control methods typically involve the use of calls to elicit coyote vocal responses or approaches. Calling and shooting relies on stimulating coyotes to approach a playback site, where they can be shot. Denning typically uses calls to pinpoint the location of active dens, after which the site is visited and the coyotes are killed (Chapter 1). Aerial gunning is often conducted in a nonselective manner (shooters in planes kill all coyotes that they find), but a common aerial gunning strategy follows the denning approach by using ground crews to direct the plane towards vocal responses (Wade 1976, Mason et al. 2002). However, the selectivity and efficacy of calling-based methods has not been evaluated with rigorous experiments. Research into the operational efficiency of these methods is badly needed, as is information about the best conditions and playback types for selectively calling alpha coyotes. This chapter addresses the latter issue by investigating coyote responses to audio playbacks.

### **Coyote Responses to Playback**

Trappers and biologists have been calling coyotes for decades (e.g. Alcorn 1946). Calling techniques include imitating coyote howls and prey without accessories, making sounds with the help of small reed-based callers, or (more recently) using sophisticated electronic speakers that store a variety of calls and can be operated by remote control. People who use calling for depredation management believe that a host of factors affect coyote responsiveness. These factors include call type, weather, barometric pressure, season, sex, and individual personality (Beaudette 1996).

Observational studies have shed some light on the purpose of coyote howls plus some of the factors that affect coyote vocalization patterns. Barks and howls from individuals correspond to agonistic behavioral contexts, but may also serve to coordinate activities among separated group members. Group vocalizations appear to strengthen group bonds and notify other packs about territory occupancy (Camenzind 1978, Lehner 1978). Gese and Ruff (1998) found that transient coyotes did not howl, and that alphas vocalized more than betas. They also noted that coyotes howled more along the periphery of their territories and during the breeding and dispersal seasons. In addition, when resident coyotes evicted territorial intruders the events were typically followed by vocalizations and scent-marking at the territory boundary (Gese 2001). These findings provide strong support for the idea that howling functions in territory maintenance and defense.

The research on spontaneous vocalizations indicates that howling is most common during the dispersal and breeding seasons (approximately October to February) and that vocalization rates peak around sunrise and sunset (Laundré 1981, Walsh and

Inglis 1989, Gese and Ruff 1998). There is considerably less agreement on other factors affecting coyote howling. For example, studies investigating the common perception that coyotes howl more when the moon is bright have either found no lunar effect (Walsh and Inglis 1989) or have found that group howling was negatively correlated with the moon's brightness (Bender et al. 1996).

Most research examining coyote responses to audio playback has focused on vocal responses, since howls are easily detected and have potential utility for estimating coyote abundance. One study of siren-elicited howling concluded that wind, rain, and some types of barometric pressure changes all decreased coyote responsiveness, but that temperature, absolute humidity, lunar cycle, cloud cover, and absolute barometric pressure had no effect (Wolfe 1974). Okoniewski and Chambers (1984) tried to elicit vocal responses from 14 radio collared coyotes; they succeeded in 25% of their attempts and noted that response rates were higher (but not significantly so) to human imitations of howls than to sirens. There was no effect of recent barometric pressure change, but there was a seasonal effect (adult coyotes were most likely to respond from December to March). Another study of elicited responses to human imitations (Gaines et al. 1995) noted greater responsiveness at dusk and dawn, was successful on 10% of howling attempts, and found that the sex of the person howling was not important.

Fulmer (1990) is the only person I am aware of who attempted to investigate coyote vocal and movement responses to playbacks. This study unfortunately suffered from a poor experimental design; the most glaring problem was the determination of movement responses based on signal changes heard by 1 observer over a short (15 minute) period. People who call and shoot coyotes have reported that it takes up to 35

min (Alcorn 1946) or 40 min (Beaudette 1996) for coyotes to approach. In addition, signal changes are inappropriate as a measure of coyote movements because many factors influence signal strength and steadiness. A steady signal generally indicates a stationary animal, but elevation has a dramatic effect on signal steadiness. If the tracker or the coyote is at a high point, there will be no movement detected even if the coyote is moving rapidly. In addition, signal amplitude and variability are strongly affected by slight movements of the animal, small elevation changes, terrain, cover, and loose equipment connections. While it is possible for a single tracker to determine azimuth changes over time, these measurements are prone to error and unconscious bias when the radio signal is unsteady (B. R. Mitchell, personal observations).

Fulmer (1990) played group vocalizations to 15 radio collared coyotes (10 known to be territorial) over the course of a year, and found that coyotes vocally responded 42% of the time. This response level was independent of biological season, month, time of day (based on 4 time periods between 1600 and 0900 that did not take sunrise or sunset time into account), and group vocalization type (group yip-howl versus group howl [Lehner 1978]). Environmental factors like wind, moonlight, barometric pressure, humidity, and precipitation also had no effect on the vocal response rate. There was, however, a trend towards increased vocal responses to playbacks within an individual's home range, and coyotes were more vocally responsive to group yip-howls than group howls during the pup-rearing season (16 May to 15 September). Fulmer reported that coyotes were more likely to move when playbacks were within their home range, and that there was more movement at wind speeds between 8 and 16 km/hr than at higher or lower

wind speeds. Season, time, and other environmental factors had no effect on movement responses.

The existing coyote playback studies are all hampered by a lack of multivariate analysis. The univariate (sometimes bivariate) approaches used in these papers failed to adjust for the confounding influences of multiple predictor variables and probably masked or overemphasized some of the trends in the data sets. Nevertheless, the research indicates that coyote responses to audio playbacks may be influenced by playback type, location of playback relative to home range boundaries, season, playback time, wind, rain, and barometric pressure changes.

The objective of my research was to evaluate the principal factors affecting coyote vocal and approach responses to playback. Some of these factors – social status, sex, position of playback relative to home range boundaries, and whether individuals were more likely to approach after a vocal response – stemmed from the coyotes themselves. Other variables were under experimental control, and included type of playback, playback time, and biological season. A final group of factors was essentially environmental or random: wind speed, barometric pressure and trend, lunar phase, and whether coyotes in the area vocalized within 5 minutes of a playback. The importance of these variables was assessed using multivariate logistic regression within a framework of multimodel selection and model parameter averaging (Burnham and Anderson 2002). Because my aim was to improve the efficacy and selectivity of techniques employing audio playback to control problem coyotes, the ultimate goal of this study was to determine whether there were conditions or playback types that selectively stimulated vocal and approach responses by alpha coyotes. My working hypothesis was that

selective responses would be most likely to realistic playbacks (e.g. actual coyote vocalizations instead of sirens) because they come closer to mimicking a territorial intrusion by competitors. These playbacks would be even more effective if they took place at times and during conditions when dominant coyotes were most likely to hear vocalizations and aggressively defend their territories (e.g. near dawn during the breeding season).

## **METHODS**

### **Study Site**

Field work was conducted on the Gray Davis Dye Creek Preserve (DCP) in northern California (Figure 15). This 15,000-ha site was managed by The Nature Conservancy; the western third was on the floor of the Sacramento Valley, and the rest was Sierra foothills and included some steep canyon terrain. The climate was Mediterranean, with hot, dry summers and cool, wet winters. There were permanent riparian zones to the north and south of the preserve, and it was cut across the middle by an additional riparian zone. The western boundary of the DCP bordered a low-density suburban area and small ranches. The habitat on the preserve consisted of grassland on the western portion, grading into increasingly dense blue oak woodland to the east.

### **Coyote Capture and Processing Procedures**

Out of 130 coyote captures between March 1998 and July 2002, 110 different individuals were caught and 92 were collared (including 3 with GPS collars, and 3 with GPS plus VHF collars). From March to October 1998, coyotes were caught primarily with padded leghold traps, and occasionally by neck snares with stops. Due to a state ban on leghold traps that began in November 1998 (California Fish and Game Code 1998), all

subsequent captures were with snare devices. Traps were checked daily, soon after sunrise, and a second check was conducted in the mid-afternoon during extreme weather conditions. Captured coyotes were physically restrained with a noose pole before being removed from the trap and transferred to a canvas bag. Processing was occasionally done at the capture site, but typically individuals were transported to a nearby building.

Once at the processing site, the coyote was chemically immobilized using ketamine and xylazine in a 5:1 ratio or physically immobilized with stretch bandages around the hind legs, fore legs, and muzzle. Drugs were normally used only if there was an attempt to pull a lower premolar for cementum annuli analysis (most adult coyotes in 1998 and 1999). Coyotes were then sexed and fitted with a VHF radio collar (ATS, Isanti, Minnesota, USA) or a GPS collar (Televilt GPS-Posrec 300, Telemetry Solutions, Concord, California, USA). Animals were ear tagged with numbered tags, and evaluated for general body condition and reproductive condition. Age was estimated by tooth wear (Gier 1968), and coyotes were checked for ectoparasites. Up to 10 mL of blood was drawn from the popliteal vein for disease research and surveillance. Beginning in 2001, 2 mL of the blood was transferred to an EDTA tube and frozen as a genetic sample; prior to this time tissue samples were obtained with a leather punch from the skin flap at the base of the ear.

After processing, coyotes were placed in a canvas bag and physical restraints were removed. Animals were then released close to their capture site. If chemical immobilization was used, individuals were allowed to recover for an hour before release, and they were watched after release to ensure that they found a safe place to rest if they were still affected by the drugs.

## **Pack Membership and Social Status**

*Data set of independent coyote locations.*--I developed a data set of reliable and independent coyote locations that was suitable for home range analysis and for evaluating pack membership and social status. The data originated from a variety of different location methods, each with different positional errors, limitations, and biases (Appendix 4). Capture locations were based on GPS data, and were within 10 m of the true location. Automated receiver data had an error of less than 100 m, and coyote sightings had an estimated positional error near 100 m. Telemetry error was similar for ground-based and aerial telemetry at approximately  $270 \pm 180$  m ( $\bar{x} \pm SD$ ). This level of error was less than 10% of the 3 to 4 km diameter of coyote territories at the DCP, so the accuracy was sufficient for delineating approximate territory boundaries and space use patterns. Mortality locations were visited with a GPS whenever possible; otherwise they were mapped using telemetry. Locations were not used in this chapter if they were collected within 4 hours of a more accurate observation.

The final location data set included 4,444 independent coyote positions. Overall, 82% of the locations were from ground-based telemetry. Visual sightings accounted for 8% of locations, and the remaining methods each contributed less than 3% of the locations. Only 59 (1.3%) locations were between 4 and 8 hours of a previous location for the same animal.

Ground-based telemetry required a minimum of: (1) 3 bearings; (2) all bearings taken within a 2-hr period (87% of locations were completed in 60 min or less); (3) spread of bearing angles greater than 45 degrees (low angles produced locations with high error along the bearing axis); (4) locations placing animals at canyon mouths had to



include at least 1 bearing from high ground; (5) error ellipse for the location less than 30 ha for triangulations calculated using LOCATE II (V. Nams, Truro, Nova Scotia, Canada); and (6) bearings used in a fix had to be consistent with bearings that were not used (allowing for bounce, distance to animal, and coyote movements). These criteria were occasionally relaxed if coyotes were in inaccessible locations or if at least 3 researchers took bearings simultaneously.

*Determination of social status and pack membership.*--I determined social status (alpha, beta, pup, or transient) and pack membership by first plotting each individual's locations on the Dye Creek Preserve GIS. The animal was considered a transient if there were long periods without locations, if the coyote showed wide movements, or if there was a tendency to stay at the boundaries of known territories. The animal was considered territorial (alpha, beta, or pup) if most locations fell within a single territory. I looked for transitions between territorial and transient status by mapping locations for 2 to 3 months at a time.

The location information was supplemented with capture data and behavioral observations. Age and female reproductive condition (i.e. lactating or enlarged nipples) were used to make initial determinations of whether individuals were alphas, betas, or pups (pups became betas on 1 October of the year they were born). These determinations were modified based on behavioral observations of interactions with other individuals. For example, a male was classified as an alpha if he spent a majority of his time in close association with the pack's breeding female, but was a beta if he was seen consorting with a subordinate female in a different pack during the mating season (because infidelity had never been reported for mated pairs). If females showed a transient movement

pattern, they were classified as transients even if they showed signs of breeding when captured. Regular association with pups was also used as an indication of alpha status. If a coyote died during the study, altered social status of surviving individuals was used as evidence that the coyote was dominant. Status and pack determinations were verified using relatedness values and genotypes obtained from 9 microsatellite loci (C. L. Williams, National Wildlife Research Center, unpublished data).

### **Playback Trials**

*Playback stimuli.*--All playback stimuli were recorded using a Tascam DA-P1 digital tape recorder (DAT) (TEAC America, Montebello, California, USA) with a phantom powered Sennheiser MKH 70 shotgun microphone (Sennheiser Electronic Corporation, Old Lyme, Connecticut, USA). The 9 distinct playbacks used for the experiment fell into 4 general categories: solo coyote (2 playbacks), group coyote (2 playbacks), human-produced imitations of coyotes or prey (4 playbacks), and siren (1 playback) (Figure 16).

Playbacks consisted of 2 segments, each approximately 30 seconds long and separated by a silent period with a randomly determined duration of 61 to 80 seconds.

Solo 1, Group 1, and Group 2 were recorded in July 1998 at the US Department of Agriculture, Wildlife Services, National Wildlife Research Center (NWRC) field station in Logan, Utah. The recording distance was between 5 m and 30 m. Solo 2 was recorded on the DCP from an uncollared coyote that approached a pilot study playback in August 1999; the recording distance was approximately 300 m. Human 1, Human 2, and Human 4 were produced by Dairen Simpson (Santa Clara County Vector Control, San Jose, California, USA) using a variety of calling devices. They were recorded in February 2000 from a distance of 5 m in annual grassland habitat on a ranch in Santa

Clara County, California. Human 3 and Siren were recorded on the DCP in March 2000 at a distance of 5 meters from the sound source. Human 3 was produced by John Fry (United States Department of Agriculture, Wildlife Services) using reed-based callers, and Siren was produced by a truck-mounted, police-style siren.

*Experimental design.*--Playback trials were conducted on the southwest portion of the DCP, where the majority of collared resident coyotes lived. A 500-m grid of 108 playback sites was constructed to avoid the steepest terrain and overlap several known territories (Figure 17). The playback location for each trial was randomly determined, with the limitation that a playback could not be within 1.5 km of the previous playback or 1 km of the playback before that. The distance limitations prevented playbacks from being conducted near each other on successive days.

For each trial, a playback time was selected from 5 possibilities that ranged from 3 hours before sunrise to 1 hour after sunrise. A playback type was also selected; playbacks could be 1 of the 9 playback stimuli or a silent control. Playback types and times were randomly selected without replacement for each set of 50 trials so that all possible combinations were included.

Weather permitting, 4 trials were conducted each week between 7 March 2000 and 5 April 2001, for a total of 212 trials. Trials were cancelled in the event of high winds (greater than 25 km per hour) or rain; trials were also cancelled during the final week of October to avoid conflicting with deer season on the DCP.

*Field procedure.*--Three researchers were involved in every trial; the playback leader was at the playback site and 2 others were at wing positions at least 1.0 km from the playback site and each other. Wing position locations were chosen to be places where telemetry

was likely to cover a radius of 2.0 km around the playback site. Researchers used all-terrain vehicles (ATVs) on preserve roads to get close to their assigned station; the rest of the distance was covered on foot using red headlamps. In addition to telemetry gear, one wing person and the playback leader had a DAT and shotgun microphone to record coyote vocal responses. The playback site also had an automated receiver (Lotek SRX 400 or SRX 400A, Lotek Wireless, Newmarket, Ontario, Canada) programmed to detect approaches closer than about 250 m. The playback system was a portable CD player connected to an Explorer PB-2500 speaker (Anchor Audio, Torrance, California, USA). The playback site researcher carried his or her gear from the nearest road using a frame pack, and navigated to within 100 m of the designated playback site (real-time GPS was only accurate to 100 m at the beginning of the experiment). Playback sites were shifted up to 50 m in some cases to avoid wildlife ponds and to take advantage of available cover.

All 3 researchers were at their trial sites with equipment set up by 70 minutes before playback. Each person cycled through the list of collared coyotes and radioed bearings and signal strengths to the playback leader, who plotted rough triangulations and determined which coyotes were nearby. Between 2 and 6 coyotes were then tracked at set intervals until playback. The tracking interval ranged from 5 minutes when 2 coyotes were tracked to 15 minutes for 5 or 6 animals. The playback speaker was directional, and was aimed towards the majority of the trial focal animals by the playback leader. During playback and for 2 minutes afterwards all researchers listened for vocal responses (and took bearings on what they heard) before resuming telemetry efforts. Coyotes were then monitored for an additional hour at the pre-playback tracking interval, after which all

researchers cycled through all frequencies one final time. Whenever possible, coyotes were tracked visually using binoculars or spotting scopes.

*Data summary.*--The playback leader was responsible for triangulating locations for the telemetry data and vocal responses using LOCATE II. Trial data were then displayed using ArcView GIS 3.2 (ESRI, Redlands, California, USA) and reviewed by the entire research team. The reliability of the data was discussed along with additional observations by team members. Because data ambiguity sometimes made decisions about movement responses difficult, the data were discussed until a consensus was reached regarding the responses of each coyote.

A vocal response was defined as vocalizations coming from the location of a collared coyote any time between the start of playback and 2 minutes after the playback ended. This means that vocal responses could have come from the collared individual or from an animal near the collared coyote. The movement response was an approach if the coyote showed directed movement towards the playback site that was a change from its pre-playback behavior. Approaches did not have to come within a specific distance of playback because playback sites were obvious (e.g. with a standing researcher conducting telemetry) and it is likely that coyotes could detect playback sites and researcher presence from a considerable distance. The movement response was a non-approach if the coyote retreated or did not change behavior. If there were not enough good data to judge the animal's movement, that animal was excluded from the trial's movement data.

The criterion for an approach was not more stringent because coyotes rapidly habituated to the experimental design and stopped approaching closely (i.e. within 250 m). During the first month of research (19 trials), there were 9 close approaches (21% of

the 43 data records, where a record corresponded to the response of 1 coyote during 1 trial). This contrasts with the remaining 12 months of research (293 trials), during which there were only 18 close approaches (4% of the 405 data records). Collared pairs of coyotes closely approached playback together only 6 times; 4 were during the first month of trials, and 2 more were in the following 2 months. The decreased close approach rate was not a seasonal effect, because trials were conducted during the same month-long period in the following year and there were no close approaches.

Habituation was evident in other measures of coyote responses, but was not as severe. For example, there were 16 approach responses (37% of 43 records) during the first month of research and 84 approach responses (21% of 405 records) during the remainder of the study. Vocal responses showed a similar drop after the first month, declining from 17% of 47 records to 8% of 528 records.

*Predictor variables.*--Coyote-specific variables included sex, social status (alpha, beta, or transient), whether the coyote responded vocally to playback (only for approach response analyses), and whether playback was inside or outside the coyote's home range (playback was outside if it was beyond the 90% probability contour). Fixed kernel home ranges were constructed for each coyote using KERNELHR 4.27 (Seaman et al. 1998) with least-squares cross-validation and a 100-m cell size. Depending on the number of locations available, home ranges were either lifetime, calendar year, or seasonal (pups present, 16 April to 30 September; pups absent, 1 October to 15 April). I used the home range that covered the shortest period of time (i.e. seasonal home ranges were preferred), included the date of playback, and was based on at least 30 independent locations. Nine coyotes (out of 34 involved in playback trials) had between 16 and 28 independent

lifetime locations. Lifetime home ranges were constructed for these individuals as well, even though these sample sizes were possibly not sufficient for accurate estimation (Seaman et al. 1999, Powell 2000). Only 7.8% of vocal response records and 6.9% of approach response records originated from coyotes with less than 30 lifetime locations.

Experimental variables were noted for each trial. These variables included playback stimulus (solo, group, human, siren, or control), time of playback relative to sunrise, and biological season. Seasons were breeding (1 January to 15 April), whelping (16 April to 15 June), rearing (16 June to 30 September), and recovery (1 October to 31 December).

Wind speed was measured at the time of playback by the playback leader, using a Kestrel 1000 wind meter (Nielsen-Kellerman, Chester, Pennsylvania, USA). The wind speed was categorized as low (less than 5 km per hour) or high. Researchers also noted whether they heard coyote vocalizations during the 5 minutes before playback. Moonrise and moonset were obtained from the United States Naval Observatory internet site ([http://aa.usno.navy.mil/data/docs/RS\\_OneYear.html](http://aa.usno.navy.mil/data/docs/RS_OneYear.html)) and lunar phase information was estimated from an internet phase calendar (<http://www.stardate.org/nightsky/moon/>). The moon was considered “up and bright” if its phase was between first quarter and last quarter and the playback time was between moonrise and moonset; otherwise the moon was “down or dim”.

Wolfe (1974) reported that recent barometric pressure changes affected coyote responses to playback, so I used a portable weather station (Econologger, Rainwise, Bar Harbor, Maine, USA) that was set up within the experimental area to record the barometric pressure in millibars at 30 minute intervals. Because the station was

inoperable for approximately 3 months of the study, data from the National Weather Service station at the Red Bluff airport (18 km WNW of the DCP) were used to supplement on-site data. The correlation between the pressure at Red Bluff and the DCP was 0.97, based on over 25,000 observations taken within 10 minutes of each other. The Red Bluff readings were converted to estimates of the missing DCP data using the regression equation: 136.45 plus 0.8506 times Red Bluff pressure. For each trial, the DCP barometric pressure reading closest to the time of playback and the net barometric trend (change in pressure over the 6 hours before playback) was recorded. Because there were times when neither weather station collected data, 14 trials lacked barometric pressure information. Instead of eliminating these trials from all analyses, pressure was ignored in the initial confirmatory analyses. Trials missing barometric pressure data were then deleted from the data sets before the exploratory analyses.

### **Data Analysis**

*General approach.*--Data for vocal responses and movement responses were analyzed separately using binary logistic regression within an information-theoretic framework. I followed the approach described in Burnham and Anderson (2002) for developing and evaluating a set of candidate models. I used the small sample Akaike's Information Criterion ( $AIC_c$ ) as my estimator of Kullback-Leibler distance because the global models had ratios of sample size to number of parameters that were below 40 (Burnham and Anderson 2002: 66). The Akaike's Information Criterion (AIC) is based on the negative log likelihood and the number of model parameters, and  $AIC_c$  adjusts the AIC at small sample sizes. For a given model set, the model with the lowest  $AIC_c$  is the most parsimonious model. Each data set was analyzed using a confirmatory (a priori)



procedure that was followed by an exploratory (post hoc) analysis (Burnham and Anderson 2002: 143-148). Detailed information about model set development is provided in Appendix 5.

*Confirmatory analyses.*--For the confirmatory phase, I developed initial model sets for vocal and approach responses without examining the data; the models were based on expected variable importance as predicted by previous research and natural history studies. This was followed by data set diagnostics, which included a check for contingency table zero cells that would hamper logistic regression (Hosmer and Lemeshow 2000: 93). I used JMP IN 4.0 (SAS Institute, Cary, North Carolina, USA) to examine univariate plots of variables against the outcome to verify my predictions of variable importance. Then I modified the initial model set based on the previous 2 steps. For example, my vocal response confirmatory analysis excluded wind speed due to a zero cell (i.e. coyotes never responded vocally in high wind), and because season was clearly less important than predicted its prevalence was reduced in the model set. Finally, I fit the global model using SAS 9.0 (SAS Institute, Cary, North Carolina, USA) and examined its goodness-of-fit via the Hosmer-Lemeshow test (Hosmer and Lemeshow 2000: 147-151) and a variety of residual plots (Hosmer and Lemeshow 2000: 167-186). Specifically, I used SAS to calculate the change in the deviance ( $\Delta D$ ) and chi-square ( $\Delta\chi^2$ ) statistics that would occur if a data record (i.e. 1 coyote's response during 1 trial) were removed. SAS also calculated C, a confidence interval displacement statistic that estimated the influence of each observation. All 3 residual statistics were plotted against the estimated logistic probability to help me identify outliers and influence points.

The global model for the vocal response confirmatory analysis did not fit and had several extreme outliers. Two of these clearly stemmed from erroneous data and were removed, and the subsequent global model did fit the data. The remaining outliers for the vocal response confirmatory analysis and for all other analyses were retained because there was no evidence of any problem with the observations.

After verifying global model fit, the entire model set was fit using SPSS 11.5 (SPSS, Chicago, Illinois, USA).  $AIC_c$  and Akaike weights were calculated for each model. The Akaike weight of a model is the weight of evidence (on a scale of 0 to 1) in favor of a given model being the best model in the set (Burnham and Anderson 2002). Models with Akaike weights below 0.01 were removed from the set (and weights were recalculated for the remaining models). For each parameter in the model set, I calculated model averaged parameter estimates  $\hat{\beta}$  and  $\tilde{\beta}$ , and the unconditional variance estimate  $\text{var}(\hat{\beta})$  (Burnham and Anderson 2002: 151-152, 162).  $\hat{\beta}$  is biased towards higher absolute values when a parameter does not appear in all models in a set, while  $\tilde{\beta}$  is unbiased but lacks a variance estimator (Burnham and Anderson 2002: 151-153, 252-254). I report all 3 estimates but base my inferences and confidence intervals on  $\tilde{\beta}$  and  $\text{var}(\tilde{\beta})$ ; this means that parameter estimates are always unbiased but variance estimates are high (conservative) when a parameter does not appear in all models in the set.

Because the units of logistic parameter estimates (change in logged odds) do not have an intuitive interpretation, I computed the odds ratios of the parameter estimates and their associated 90% confidence intervals by exponentiating the parameter estimate and the endpoints of the confidence interval. I also calculated probability estimates and 90%

confidence intervals for important combinations of variable values (Hosmer and Lemeshow 2000: 40-42). This calculation required a covariance matrix, and since there is no straightforward way to calculate a model-averaged covariance matrix I used the matrix for the model containing only the important variables.

*Exploratory analysis.*--Exploratory analyses allowed me to investigate the importance of barometric pressure and alternative functional forms and interactions that were not predicted a priori. This type of analysis is not as statistically rigorous as a confirmatory study; exploratory results should be taken with a grain of salt since they are optimized to fit a particular data set and may not be repeatable. The procedure followed the confirmatory analysis methods, except that the model set was derived differently. The initial model set was the confirmatory set, which was re-fit because observations were deleted. The  $AIC_c$  best model was then used as the starting point for guided model building, where 1 variable or interaction at a time was added or removed. This was essentially a manual stepwise model selection procedure. The final model set included all models within 2  $AIC_c$  units of the best model (1  $AIC_c$  unit for interaction parameters), and model averaging was based on this set after goodness-of-fit tests confirmed the fit of the global model.

## **RESULTS**

### **Sample Sizes and Initial Data Review**

Between 7 March 2000 and 5 April 2001, 34 individual coyotes participated in 212 playback trials. Because multiple coyotes participated in each playback trial, the final vocal response confirmatory data set contained 575 coyote records, 51 of which were responses. The number of records per coyote was skewed (Figure 18). Figure 18

has 37 columns because 3 of the 34 coyotes changed status; 1 column is empty because of a transient that did not contribute any vocal response records. Some individuals clearly dominated the data set; 62% of response records were from 8 coyotes, and coyote 5940-M was responsible for 75% of beta male data.

Univariate contingency table analyses showed that coyote sex, coyote social status, playback type, and wind speed were all important predictors of coyote vocal responses ( $p < 0.001$  for each variable). Coyotes never vocally responded in high wind (compared to a 9% response rate when wind speed was below 5 km per hour). Males vocalized 14% of the time they were involved in playback trials, while females only responded 5% of the time. Transients only responded 1% of the time, while vocal response rates were 12% for alphas and betas. Coyotes never responded to control trials; they occasionally responded to solo coyote vocalizations, the siren, and human imitations (2%, 5%, and 7%, respectively); and they regularly vocally responded to group coyote vocalizations (23% response rate). Vocal response rates did not vary depending on the presence of vocalizations before playback, nor did they vary for different playback locations, biological seasons, and lunar conditions ( $p > 0.10$  for all variables).

The approach response data exhibited a skewed distribution of records per individual coyote similar to the skew present in the vocal response data. The data set included 448 total records and 100 approach responses (Figure 19). Nine individuals were the source of 68% of the records, and 5940-M was again responsible for 75% of the beta male data.

Univariate contingency table analyses showed that coyote social status, playback type, and the presence of vocalizations before playback were important predictors of

coyote approach responses ( $p < 0.05$  for each variable). Transient coyotes had low approach rates (13%), while territorial coyotes had approach rates approximately twice as high (24% for alphas and 29% for betas). Approach rates also varied depending on playback type, with control trials (10%) and solo coyote vocalizations (14%) attracting fewer coyotes than the siren (24%), human imitations (26%), and group coyote vocalizations (28%). Coyotes were more likely to approach playback sites when there were no natural coyote vocalizations preceding playback (the approach rate increased from 11% to 23%).

Playback location and biological season were potentially useful for predicting coyote approach responses ( $p = 0.06$  and  $0.09$ , respectively). Coyotes approached playbacks within their home range 25% of the time, and only approached 17% of the time when playbacks were outside of their home range. The pup-rearing and recovery seasons were associated with a 17% approach rate, while coyotes approached playbacks during the breeding and whelping seasons 28% of the time. Coyote sex, playback time, wind speed, lunar condition, and vocal responses to playback were not associated with differences in the approach rate ( $p > 0.10$  for all variables).

The vocal response exploratory data set contained 403 records (43 responses) after transients and trials lacking barometric pressure data were removed. Transients were eliminated because the presence of only 1 vocal response by a transient during the experiment produced zero cells in all models containing a social status interaction term. The data set included records from 19 coyotes, with 7 individuals contributing 75% of the data. The approach response exploratory data set contained 419 records (96 responses)

from 31 coyotes after trials lacking barometric data were removed. Ten individuals in this data set contributed 76% of the information.

It was not possible to correct for the skewed number of records per individual coyote in the data sets, so inferences based on these data are only widely applicable to the extent that the relatively small numbers of coyotes involved behaved like other coyotes with the same sex and social status.  $AIC_c$  values reported in the following results were calculated using the number of records in the appropriate data set.

### **Confirmatory Vocal Response Analysis**

The vocal response data set excluded control trials (82 records) and trials with “high” wind (greater than 5 km per hour, 96 records) because coyotes never responded in these conditions. Low wind speeds and the presence of an actual playback were clearly needed for eliciting coyote vocal responses, but including control trial and high wind data in the logistic regression models would have produced zero cells and numerical problems in the analysis (Hosmer and Lemeshow 2000: 93).

The model containing only social status, sex, and playback type had the greatest support in the final model set, with an Akaike weight above 40%. The model that added vocalizations before playback also had a high weight of evidence (27%), while the remaining models had weights of 8% or lower (Table 26). Biological season and the interaction of social status by playback type were not present in the final model set; models with these variables always had low Akaike weights (Appendix 5).

Parameter estimates for social status and playback type (compared to the reference groups of transient coyotes and siren playbacks) indicated that both of these variables were important (Table 27). The odds of a vocal response by transients were

over 15 times lower than for betas and 18 times lower than for alphas. Solo playbacks had odds of eliciting vocal responses that were 2.4 times lower than siren playbacks, human playbacks had similar efficacy to the siren, and group playbacks were associated with a nearly 6-fold increase in the odds of response when compared to the siren.

Sex was also clearly important; the odds of a male vocal response were 2.5 times greater than the odds of a female response (Table 27). The presence of vocalizations within 5 minutes of playback may have increased the responsiveness of collared coyotes, but the 90% confidence interval of the parameter estimate overlapped zero. None of the remaining parameters were important, although there was a trend towards increased vocal responsiveness 2 hours and 1 hour before sunrise (compared to the reference time of 3 hours before sunrise).

A plot of the probability of vocal response at different parameter values makes it easier to see the impact of the important variables. Status, sex, and playback type had a dramatic effect on the probability of a vocal response to playback (Figure 20). Transients almost never responded, while alpha and beta males responded vocally to about 35% of group coyote playbacks. Females tended to vocalize less than half as often as males, and siren and human playbacks were less effective than group coyote playbacks but more effective than solo playbacks. The likelihoods in Figure 20 assumed no vocalizations before playback, playback 3 hours before sunrise, moon down or dim, and playback outside of the responding coyote's home range. Changing these assumptions would have resulted in slight changes to the probability estimates.

### **Exploratory Vocal Response Analysis**

The final model set for the exploratory vocal response analysis contained 13 models with Akaike weights ranging from 0.04 to 0.11 (Table 28). All of the models contained social status (alpha and beta only), sex, playback type, lunar phase, and the interaction between social status and sex. Net barometric change (change in pressure over the 6 hours preceding playback) and time of morning (“before sunrise” or “sunrise and later”) were each present in more than half of the final model set.

Social status, sex, and playback type were again the most important parameters predicting the logged odds of a vocal response to playback (Table 29). The odds of an alpha vocal response were 5.6 times greater than the beta odds, and males had odds 16.6 times greater than females. These effects were modified by a strong negative interaction between status and sex that decreased alpha male vocal response odds to a level near the alpha female odds. The odds of vocal response show the same pattern relative to playback type that was found in the confirmatory analysis: the odds of response were lowest to solo playbacks and highest to group playbacks, with low odds of response to siren (the reference group) and human playbacks.

Lunar condition was also important, with the odds of vocal response 3.0 times greater when the moon was up and bright than when it was down or dim (Table 29). Playback time may have influenced the chance of a vocal response; the estimated odds of a vocal response at sunrise or later were 0.5 times the odds of a response before sunrise, but the 90% confidence interval of the estimated logged odds encompassed zero. In addition, net barometric change potentially influenced vocal responses. A 3.0 millibar increase in the net barometric change (e.g. from -1.4 to +1.6 millibars, the 10% and 90%



quantiles) corresponded to an estimated 1.49 times higher odds of vocal response but had a 90% CI of 0.81 to 2.74 times.

The predicted probability of vocal response varied considerably depending on the values of the important parameters (Figure 21). Within each playback type, beta females had the lowest response rate and beta males had the highest, with alphas slightly below the beta male level. For playbacks of group coyote vocalizations during the “best” conditions (i.e. before sunrise with the moon up and bright), this corresponded to a response rate of 11% for beta females, 42% for alpha females, 68% for beta males and 56% for alpha males. Group playbacks during “poor” conditions (after sunrise with the moon down or dim) decreased the estimated response probability by at least a factor of 2. The moon had a greater effect on this probability reduction than time; the lunar parameter estimate was 40% larger with a 50% smaller standard error than the estimated time parameter. The probabilities in Figure 21 would be slightly decreased by negative net barometric changes, and slightly increased by positive changes.

### **Confirmatory Approach Response Analysis**

The final model set for the confirmatory approach response analysis contained 15 models (Table 30). No single model was dramatically better than the others, and Akaike weights ranged from 0.02 to 0.16. Social status and playback type were present in all of the models, while biological season, playback location, the presence of vocalizations before playback, and the interaction of social status and playback location were retained in the majority of models. Playback time and the interaction between social status and playback type were not present in the final model set.

Playback type was the most important parameter predicting the logged odds of an approach (Table 31). Solo playbacks were no more effective than control playbacks (the reference group in the analysis), but the odds of an approach nearly tripled for siren and human playbacks. Group playbacks were associated with odds of approach 3.5 times greater than control playbacks. The parameter estimates for social status and playback location indicated only a slight to moderate effect on the logged odds of an approach. However, the estimates of the interaction between status and playback location suggested that territorial coyotes had a greater odds of approaching playback when the playback was within their home range.

Biological season and the presence of vocalizations within 5 minutes of playback also affected the odds of an approach response (Table 31). The odds of a vocal response were about 1.7 times lower during the rearing and recovery seasons than during breeding (the reference group) and whelping periods, while vocalizations before playback reduced the odds of an approach by a factor of 2.

Wind speeds above 5 km per hour may have decreased the odds of an approach, and the presence of bright moonlight may have increased the odds of an approach, but the 90% confidence intervals for these parameter estimates overlapped zero (Table 31). There was no evidence that coyote sex or a vocal response by the approaching coyote affected the odds of an approach.

The parameter estimates from the analysis can be converted to the probability of approach given specific levels of the important variables (Figure 22). The results were less dramatic than the vocal response findings, but response probabilities were highest to group playbacks and lowest to control playbacks. Within each type of playback,

conducting playbacks in the first half of the year (breeding and whelping seasons) at times when vocalizations did not precede playback generally tripled the probability of an approach compared to playbacks preceded by natural vocalizations during the rest of the year. The interaction between status and location is also prominent in Figure 22.

Comparing squares versus diamonds (outside versus inside home range) within a playback type reveals that approach rates are low and similar between the social statuses when playbacks are outside the home range, but that betas were almost twice as likely to approach and alphas were about 50% more likely to approach when playbacks were within the home range.

### **Exploratory Approach Response Analysis**

The final model set for the exploratory approach response analysis contained 11 models with Akaike weights ranging from 0.06 to 0.17 (Table 32). All of the models contained social status, playback type, and playback location. Vocalizations before playback, biological season (“breeding and whelping” from 1 January to 15 June, and “rearing and recovery” from 16 June to 31 December), and playback time (“sunrise and earlier” or “after sunrise”) were each present in more than half of the final model set. The prominent variables were the same as in the confirmatory movement analysis, except that playback season and playback time were more important when collapsed to 2 categories, and the interaction of status and location was not included here.

The most important parameters were playback type and social status (Table 33). The odds of an approach to group playbacks were 3.4 times higher than to control playbacks (the reference group), and the odds of an approach to siren and human playbacks were 2.6 and 2.9 times higher than to controls. The odds of an alpha

approaching playback were 2.4 times higher than the odds of a transient approach, with the odds of a beta approach slightly higher than the value for alphas.

Playback location was also important, with the odds of an approach 1.8 times higher when the playback was inside the animal's home range (Table 33). Season had an effect of similar strength; the odds of an approach were 1.6 times higher during the reference season (1 January to 15 June) than during the rest of the year. Playbacks after sunrise and vocalizations before playback were both associated with 1.8 times lower response odds, although the 90% confidence interval for vocalizations before playback slightly overlapped zero.

The plot of probabilities of an approach response was nearly identical to the plot from the confirmatory analysis, except that alpha approach rate estimates were closer to beta estimates, there was no interaction between status and location, and confidence intervals were smaller (Figure 23). As with the confirmatory analysis, approach rates increased as playback changed from control to siren to group coyote vocalizations. In addition, approach rates were always higher when playbacks were within the animal's home range (diamonds versus squares). The effects of season, time, and vocalizations before playback were each of similar strength, and were combined into a comparison of "best" versus "worst" conditions (gray versus white bars and symbols). The probability of an approach response when conditions were optimal – during the first part of the year, at sunrise or earlier, and with no vocalizations before playback – were always 3 to 4 times higher than the probability of approach when conditions were poor.

## Summary

All analyses confirmed the importance of social status and playback type for predicting coyote responses to playback. Transients were always less likely than alphas and betas to approach or vocalize after a playback. Alphas and betas generally responded similarly to playbacks, except that the vocal response exploratory analysis suggested that beta females were less likely to vocally respond than other territorial coyotes. Coyotes were least likely to respond to control playbacks (in fact there were no vocal responses during control trials), and they were most likely to respond to group coyote playbacks. Of the other playbacks, solo coyote vocalizations were least likely to generate a response, while the siren and human imitations had higher response rates (and the siren and human playbacks had approach response rates near the level found for group coyote playbacks).

Coyote sex was important for predicting vocal responses (males responded more often than females), but was not important for predicting approach responses. In contrast, biological season, vocalizations before playback, and the location of the playback relative to home range boundaries were all important for predicting coyote approaches, but were not useful for predicting vocal responses. Higher approach rates were associated with the breeding and whelping seasons (1 January through 15 June), a lack of vocalizations before playback, and playback sites within home range boundaries.

The exploratory analyses suggested that playback time was important when the data were grouped: vocal responses were most likely before sunrise, and approach responses were most likely at sunrise or earlier (times ranged from 3 hours before to 1 hour after sunrise). The exploratory results also suggested that vocal responses were more likely when the moon was up and bright (as opposed to down or dim).

## **DISCUSSION**

### **Vocal Responses to Playback**

The results bore out my prediction that selective vocal responses would be most common in response to realistic playbacks. The lack of vocal responses by transients mirrored observations by Gese and Ruff (1998) that this social class does not vocalize; these individuals were probably trying to avoid attracting the attention and aggression of resident coyotes. Playbacks of group vocalizations (group howls or group yip-howls) yielded the highest overall response rate. The 2 types of group vocalizations have overlapping purposes: both are thought to function in group bonding and territorial displays, but group howls are less intense and may also coordinate group reunions (Lehner 1978). Playbacks of either type of vocalization should elicit similar vocal responses from territorial coyotes, as they affirm occupancy of their territory and warn the potential intruders. Solo playbacks (primarily barks but including occasional howls [Figure 16]) had the lowest response rate. Barks are probably a low-level agonistic threat or alarm (Lehner 1978, Chapter 2), and study coyotes may not have considered these playbacks threatening enough to warrant a response.

The response rates to the siren and human imitations of coyote howls and prey were intermediate between the rates for solo and group vocalizations. Coyotes probably did not perceive these playbacks as conspecifics, even when they were imitations of coyote howls; there were numerous spectrographic differences between the different playbacks (Figure 16) that the study animals could likely perceive. Coyotes occasionally challenged researchers at the DCP with approaches and bouts of barking and howling (B. R. Mitchell, personal observations), and Harrington and Mech (1979) were challenged by

wolves several times. Coyotes may perceive humans as potential competitors, and they may be interpreting and responding to siren and human playbacks as if they were interspecific aggressive displays. Alternatively, nearby coyotes probably recognized that the playbacks were not coyote vocalizations, but distant coyotes may have interpreted the degraded sounds they heard as howling and responded accordingly. Nearby coyotes could be responding to these distant animals, and not directly to the playback. This is similar to a phenomenon noted in Chapter 2: subject coyotes never vocally responded to playbacks, but more distant animals housed in kennels regularly responded, and subject coyotes subsequently responded to the kennel coyote vocalizations.

Vocal response rates differed by sex and did not vary across biological seasons; both of these findings ran counter to expectations based on observations by Gese and Ruff (1998). The difference in male and female response rates in my study could be due to the changed behavioral context, with coyotes responding to a playback rather than vocalizing spontaneously. Playbacks typically imitate a territorial intrusion, and responding to vocalizing invaders would increase the chance of being found and attacked. Gese's (2001) observations of active territorial defense (chasing and fighting intruders) showed that males were about twice as likely to engage intruders than females, and that beta females rarely participated in defense. The exploratory vocal response analysis showed the same pattern found by Gese: males were most likely to respond vocally, alpha females often responded, and beta females rarely vocalized. These sex and status differences likely reflect differing levels of willingness to aggressively defend the territory.

Gese and Ruff (1998) suggested that their seasonal peak in howling rates was related to reinforcement of pair bonds and increased aggression towards intruders. The seasonal invariance of elicited response rates in my study could arise if the rate of spontaneous vocalizations varied seasonally, but the probability of responding to vocalizations was constant. Howling in wolves actually serves to keep different packs from coming in contact with each other (Harrington and Mech 1983), and it has been suggested that coyotes use howling in a similar way (Lehner 1978, Fulmer 1990). Territorial coyotes may respond to vocalizations as a relatively low-cost strategy for telling neighbors and intruders that the area is occupied. If so, they should have the same rate of response across seasons if they perceive playbacks as an intraspecific or interspecific threat.

Okoniewski and Chambers (1984) reported seasonal variation in coyote responses to playback, but their statistical technique was flawed. They calculated seasonal response rates by averaging the mean responses per coyote and estimating the sample variance. Then they compared seasonal confidence intervals using an undisclosed alpha level. Such an approach might work if there were approximately equal samples per coyote and 5 or more samples per individual, but in this case 12 of 21 estimates of seasonal adult coyote response rates were based on less than 5 observations, and sample sizes within each season varied considerably. A more appropriate test of seasonal variability would be a contingency table analysis, although this approach ignores pseudoreplication by assuming that response rates do not vary between individuals. Such an analysis of Okoniewski and Chambers' data revealed no difference between seasonal response rates by adults ( $\chi^2 = 3.7$ ,  $df = 3$ ,  $p = 0.30$ ).



Wind speed was an important factor affecting vocal responses to playback, and this result was expected based on previous research (Wolfe 1974). Collared coyotes at the DCP never vocally responded when wind speeds were greater than 5 km per hour; this effect is likely a combination of decreased coyote responses and decreased ability of researchers to hear responses as wind speed increased.

The exploratory data analysis suggested that coyotes were more responsive when the moon was up and bright, playbacks were 1 to 3 hours before sunrise, and the net barometric pressure trend was increasing. The lunar effect was stronger than the time and barometric pressure effects (90% confidence intervals for the time and pressure parameters overlapped zero). These environmental variables could all reasonably affect playback vocal response rates if they corresponded to periods when coyotes were more active. Coyotes have an activity peak beginning at dusk, with another (generally smaller) peak before dawn (Andelt and Gipson 1979, Andelt 1985, Kitchen et al. 2000, Grinder and Krausman 2001). In addition, Bender et al. (1996) noted that coyotes should be more active when a bright moon enhances visual foraging. An increasing barometric pressure normally signals improving weather, so this variable may also correlate with increased coyote activity. These exploratory results need to be confirmed with an independent data set, but it is intriguing that “good” environmental conditions (i.e. moon up and bright, before sunrise, and rising barometer) were associated with a greater than 2-fold increase in predicted vocal response rates of territorial coyotes.

### **Approach Responses to Playback**

Other than Fulmer (1990), I am not aware of any studies of coyote movement behavior in response to playbacks. Within the genus *Canis*, the only systematic study of

approaches to playback was Jaeger et al.'s (1996) study of golden jackals (*C. aureus*). They compared approach and vocal response rates during the pairing-mating (December to mid-January) and denning (April, May and June) seasons. They found that approaches were more common in the denning season, there may have been a tradeoff between vocal and approach responses, and vocal responses did not appear to be used in tandem with approaches.

My results suggest that coyotes approached playbacks partly out of curiosity, and partly for territorial defense. Approaches normally stopped several hundred meters from the playback site, which was close enough to determine that a researcher was present at the site but probably not near enough for coyotes to feel threatened. The importance of curiosity is best supported by the moderate rate of approaches to control (silent) playbacks: during the breeding and whelping seasons, territorial coyotes approached about 20% of control playbacks, provided the playback time was at sunrise or earlier and there were no vocalizations immediately preceding playback (Figure 22 and Figure 23). Given the same conditions, transients approached about 10% of control playbacks. Coyotes were likely interested in human activity on the DCP, since humans were a source of food (e.g. hunters leaving animal remains) and danger (e.g. researchers setting traps or poachers shooting coyotes). Thus there were benefits to cautiously approaching and evaluating human activities that coyotes became aware of. In addition, an unknown proportion of approaches were subject to measurement error. Telemetry error and behavioral decisions unrelated to experimental playbacks could have led to the appearance of an approach towards playback, even if the coyote was unaware or uninterested in research activity.

Solo playbacks were no more attractive to coyotes than control playbacks. Solo coyote vocalizations with a high proportion of barks may not have been considered a strong enough threat to warrant an approach response. Group coyote vocalizations, on the other hand, were the most successful playback type for attracting coyotes; approaches to this playback type were more than double the rate to control playbacks, and they were slightly higher than approach rates to the siren and human imitations of coyote vocalizations and prey. Interest in group coyote vocalizations may have stemmed from a desire to combat territory intruders or curiosity about the cause of the commotion. Coyotes likely responded to the siren and human vocalizations for a variety of reasons; they may have interpreted the playbacks as a human interspecific aggressive display, they may have been curious about the disturbance, or they may have believed that some of the playbacks (e.g. imitated coyote howls) were the real thing and responded accordingly.

Social status and playback location also had strong effects on approach rates. The confirmatory analysis indicated an interaction between status and location, whereby transients responded irrespective of playback location but territorial coyotes were more likely to respond to playbacks within their home ranges. However, the confidence intervals for the interaction parameters overlapped zero (Table 31), and this interaction was not important enough to be used in the exploratory analysis. It is likely that the importance of this interaction was overestimated in the confirmatory analysis (Appendix 5), and that it was subsequently over-represented in the final model set.

Ignoring the possible status by location interaction, territorial coyotes were about twice as likely to approach playbacks as transients, and all coyotes were nearly 50% more likely to approach playbacks within their home ranges. Coyotes were probably more

comfortable approaching playbacks on familiar territory, plus they may have felt more of a need to investigate disturbances inside their home ranges and territorial coyotes may have wanted to challenge intruders. Alphas approached slightly less often than betas, perhaps indicating a lower level of curiosity or a better ability to determine that playbacks were not coyotes.

Biological season also affected approach rates. Coyotes were more likely to approach playbacks during the breeding and whelping seasons (1 January to 15 June) than during the rest of the year. This first portion of the year is when territorial coyotes are most sensitive to intrusions; Gese (2001) noted that almost all territorial chases observed during his research occurred from December to June. On the DCP, most of the higher responsiveness at the beginning of the year was probably due to enhanced territorial behavior, as alphas bred, dened, and protected their young pups. In addition, this time of year had the coldest and wettest weather, and the lowest levels of rodent prey. Energy needs may have made coyotes more likely to investigate playbacks and other disturbances during the breeding and whelping seasons. Jaeger et al. (1996) documented a higher approach rate during the whelping season than the breeding season for golden jackals, which I was not able to replicate for coyotes.

The presence of vocalizations within 5 minutes of playback reduced the chance of an approach. The lowered approach rate probably reflected the need for coyotes to choose which vocalizations to investigate. Playback time also affected approaches, but only when divided into 2 categories: after sunrise and earlier. Coyotes were less likely to approach when playbacks occurred 1 hour after sunrise. This is a similar pattern to the one seen for vocal responses, except that coyotes still approached playbacks when they

occurred at sunrise and they were less likely to vocalize at this time. Some of the reduced response rate probably stemmed from decreased activity levels after sunrise, but part was likely due to the increased ease with which coyotes could see the human presence at playback sites.

Sex, wind, and lunar condition were conspicuous in their lack of importance, since each affected vocal response rates. The most surprising of these was the absence of a sex effect. Males were expected to be more likely to approach than females, since they are more aggressive and more likely to be involved in territorial defense (Gese 2001). However, quietly approaching and observing the playback site from a distance is not risky; approaches are only dangerous when they are fast and close. Curiosity about events within their home range may have made females just as likely to approach playbacks as males; they may just not have approached as closely or aggressively.

There was a slight trend towards lower approach probabilities in “high” wind (above 5 km per hour); it was expected that coyotes would be less likely to hear playbacks, and less likely to respond, when wind speeds were higher. Part of the lack of a strong effect could be due to approaches that were occasionally based on coyotes seeing researcher activity rather than hearing playback.

Coyotes were expected to approach more often when the moon was up and bright, under the assumption that activity levels were higher at that time. Perhaps coyotes were engaged in activities (such as foraging) that made them less likely to approach when there was bright moonlight, even though they were more likely to vocally respond. Another possibility is that approaches were under-detected when the moon was up and bright.

This could occur if coyotes felt less comfortable approaching in the light, and therefore did not approach as closely, making it harder to detect the response using telemetry.

Coyotes were no more likely to approach playback after vocalizing, even though vocal responses were predicted to enhance the likelihood of an approach (by signaling territorial ownership and the willingness to defend). Jaeger et al. (1996) similarly found no link between vocal responses and subsequent approaches by golden jackals. Part of the problem in their research and mine could be the difficulty in determining the identity of a vocalizing coyote; vocal responses could come from an uncollared coyote next to the collared individual, and that individual would be undetected when he or she subsequently approached. In addition, if vocal responses are a spacing mechanism (Harrington and Mech 1979) rather than a prelude to aggression, vocal responses should decrease rather than increase the probability of an approach.

### **Management Implications**

Alpha coyotes are most commonly implicated in livestock losses (Sacks et al. 1999b), and observations of coyotes killing large prey suggest that betas (particularly beta males) may often be involved (Gese and Grothe 1995). My research shows that alpha and beta coyotes were much more likely to respond vocally and approach playbacks than transients. Provided that care is taken to conduct control efforts in the same coyote territory where depredations are occurring (e.g. by conducting playbacks within 1 km of kills), playbacks will selectively target the individuals most likely to be killing livestock.

Playbacks were much more effective at stimulating vocal responses when group coyote vocalizations (pair howls and group yip-howls) were used. In addition, playbacks

before sunrise during times when the moon was up and bright had higher estimated vocal response rates. Approach response rates were highest to group vocalizations, but the siren and human imitations of coyotes and prey had a similar efficacy. Attracting coyotes to a playback site was most successful when playbacks were inside the coyotes' territory, at or before sunrise, during the first part of the year (1 January to 15 June), and when there were no spontaneous coyote vocalizations before playback.

This study was limited by the presence of a person conducting radio telemetry at the playback site; the researcher likely prevented coyotes from approaching closely and may also have served as an object of curiosity. To address this and other important issues, an additional year of playback trials was conducted using a revised experimental procedure. This second study used a timer-operated remote playback unit that was placed the day before a trial. Data resolution was improved by adding a fourth telemetry station during the trial, and playbacks were limited to several different types of coyote vocalizations to better investigate the importance of different howl types. The findings from the second playback study will help to confirm and extend the results reported here.

My study was also affected by my use of a minimally exploited population of subject animals that were accustomed to human activities. Coyote responses to playback may differ in areas where coyotes are heavily exploited, and the best way to investigate the importance of exploitation levels (while also avoiding habituation effects) is with a thorough investigation of the operational efficacy of playback-based depredation control methods. Coyote DNA can be collected from the wounds on dead livestock (Williams et al. 2003) and then compared with genetic samples taken from coyotes killed using traps, cyanide ejectors, aerial gunning, calling and shooting, and denning. Such an operational

test is the only way to accurately gauge which methods are truly the most selective and effective for controlling coyote damage.



Table 26. Final model set for confirmatory vocal response analysis. Notation follows Burnham and Anderson (2002).

Model <sup>1</sup>	K	AIC <sub>c</sub>	$\Delta_i$	$\omega_i$
8: Status + PB Type + Sex	7	292.8	0.0	0.442
7: Status + PB Type + Sex + VB4	8	293.8	1.0	0.269
6: Status + PB Type + Sex + Time	11	296.3	3.4	0.079
4: Status + PB Type + Sex + Time + VB4 + Moon	13	296.5	3.7	0.071
5: Status + PB Type + Sex + Time + VB4	12	296.8	4.0	0.060
2: Status + PB Type + Sex + Time + VB4 + Loc + Moon	14	297.9	5.0	0.036
3: Status + PB Type + Sex + Time + VB4 + Loc	13	298.4	5.5	0.028
9: Status + PB Type	6	299.5	6.6	0.016

<sup>1</sup> VB4 = Vowels before PB, Loc = PB Location.

Table 27. Parameters for confirmatory vocal response analysis. Notation follows Burnham and Anderson (2002).

Parameter	Change in Logit or Logged Odds <sup>1</sup>				Odds Ratio <sup>1</sup>		
	$\hat{\beta}$	$\hat{\beta}$	$\text{var}(\hat{\beta})$	90% CI <sup>2</sup>	$\hat{\beta}$	$\hat{\beta}$	90% CI
Constant	-6.12	-6.12	1.49	-8.12 to -4.12	0.00	0.00	0.00 to 0.02
Beta	2.73	2.73	1.12	1.00 to 4.47	15.40	15.40	2.71 to 87.67
Alpha	2.90	2.90	1.05	1.21 to 4.58	18.09	18.09	3.34 to 97.90
Human PB	0.33	0.33	0.44	-0.76 to 1.42	1.39	1.39	0.47 to 4.15
Solo PB	-0.89	-0.89	0.72	-2.28 to 0.51	0.41	0.41	0.10 to 1.66
Group PB	1.77	1.77	0.43	0.69 to 2.84	5.84	5.84	1.99 to 17.15
Male	0.92	0.94	0.11	0.38 to 1.46	2.52	2.55	1.47 to 4.31
Vowels before PB	0.24	0.52	0.21	-0.52 to 1.00	1.27	1.67	0.59 to 2.71
PB 2 hrs before sunrise	0.13	0.46	0.26	-0.71 to 0.96	1.13	1.58	0.49 to 2.60
PB 1 hr before sunrise	0.14	0.53	0.22	-0.63 to 0.92	1.16	1.69	0.53 to 2.50
PB at sunrise	-0.01	-0.05	0.30	-0.91 to 0.89	0.99	0.96	0.40 to 2.43
PB 1 hr after sunrise	-0.11	-0.41	0.33	-1.06 to 0.84	0.89	0.66	0.35 to 2.31
Moon up and bright	0.06	0.57	0.13	-0.52 to 0.64	1.06	1.76	0.59 to 1.91
PB inside home range	0.02	0.27	0.11	-0.54 to 0.57	1.02	1.31	0.58 to 1.77

<sup>1</sup> Change in logit of 0 or odds ratio of 1 indicates no difference between the parameter and reference group.

$$^2 \hat{\beta} \pm 1.645 \sqrt{\text{var}(\hat{\beta})}.$$

Table 28. Final model set for exploratory vocal response analysis.

Model <sup>1</sup>	K	AIC <sub>c</sub>	$\Delta_i$	$\omega_i$
48: Stat + Typ + Sex + T2 + Moon + NBC + Stat*Sex + Sex*T2	11	232.8	0.0	0.108
68: Stat + Typ + Sex + Moon + NBC + Stat*Sex + Sex*T2	10	233.0	0.1	0.101
45: Stat + Typ + Sex + T2 + Moon + NBC + Stat*Sex	10	233.0	0.1	0.101
58: Stat + Typ + Sex + Moon + NBC + Stat*Sex	9	233.0	0.2	0.097
57: Stat + Typ + Sex + T2 + Moon + Stat*Sex	9	233.1	0.3	0.093
61: Stat + Typ + Sex + Moon + Stat*Sex	8	233.3	0.5	0.085
47: Stat + Typ + Sex + T2 + Moon + NBC + Stat*Sex + Stat*T2	11	233.6	0.8	0.074
53: Stat + Typ + Sex + T2 + Moon + NBC + Stat*Sex + Sex*T2 + Sex*NBC	12	233.6	0.8	0.074
49: Stat + Typ + Sex + T2 + Moon + NBC + Stat*Sex + Sex*NBC	11	233.7	0.9	0.070
64: Stat + Typ + Sex + Moon + NBC + Stat*Sex + Sex*NBC	10	233.8	1.0	0.066
51: Stat + Typ + Sex + T2 + Loc + Moon + NBC + Stat*Sex + Sex*T2	12	234.5	1.7	0.046
46: Stat + Typ + Sex + T2 + Loc + Moon + NBC + Stat*Sex	11	234.7	1.9	0.043
63: Stat + Typ + Sex + Loc + Moon + NBC + Stat*Sex	10	234.8	1.9	0.041

<sup>1</sup> Stat = Status, Typ = PB Type, T2 = Time with 2 categories (before sunrise and later), Loc = PB Location,

NBC = Net Barometric Change.

Table 29. Parameters for exploratory vocal response analysis.

Parameter	Change in Logit or Logged Odds <sup>1</sup>				Odds Ratio <sup>1</sup>		
	$\hat{\beta}$	$\hat{\beta}$	$\text{var}(\hat{\beta})$	90% CI <sup>2</sup>	$\hat{\beta}$	$\hat{\beta}$	90% CI
Constant	-5.25	-5.25	1.65	-7.36 to -3.13	0.01	0.01	0.00 to 0.04
Alpha	1.73	1.73	1.18	-0.06 to 3.51	5.62	5.62	0.94 to 33.50
Human PB	0.11	0.11	0.49	-1.05 to 1.26	1.11	1.11	0.35 to 3.54
Solo PB	-0.70	-0.70	0.75	-2.12 to 0.72	0.49	0.49	0.12 to 2.05
Group PB	2.10	2.10	0.48	0.96 to 3.24	8.17	8.17	2.61 to 25.61
Male	2.81	2.81	1.27	0.95 to 4.66	16.55	16.55	2.58 to 106.03
Moon up and bright	1.09	1.09	0.17	0.41 to 1.76	2.96	2.96	1.52 to 5.81
1 mbar net baro change <sup>3</sup>	0.13	0.18	0.05	-0.21 to 0.48	1.14	1.20	0.80 to 1.62
3 mbar net baro change <sup>3</sup>	0.40	0.55	0.14	-0.21 to 1.01	1.49	1.74	0.81 to 2.74
PB sunrise (SR) or later	-0.67	-0.95	0.70	-2.05 to 0.70	0.51	0.39	0.13 to 2.02
PB inside home range	0.03	0.24	0.14	-0.59 to 0.65	1.03	1.27	0.55 to 1.92
Alpha*Male	-2.24	-2.24	1.38	-4.17 to -0.31	0.11	0.11	0.02 to 0.74
Male*Net baro (1 mbar)	0.08	0.39	0.11	-0.47 to 0.63	1.09	1.48	0.62 to 1.89
Male*PB SR or later	0.45	1.35	0.90	-1.12 to 2.01	1.56	3.87	0.33 to 7.45
Alpha*PB SR or later	-0.08	-1.12	0.83	-1.58 to 1.41	0.92	0.33	0.21 to 4.10

<sup>1</sup> Change in logit of 0 or odds ratio of 1 indicates no difference between the parameter and reference group.

$$^2 \hat{\beta} \pm 1.645 \sqrt{\text{var}(\hat{\beta})}.$$

<sup>3</sup> Net barometric pressure change data ranges from -2.7 to +3.4 millibars.

Table 30. Final model set for confirmatory approach response analysis.

Model <sup>1</sup>	K	AIC <sub>c</sub>	$\Delta_i$	$\omega_i$
24: Stat + Typ + Seas + Loc + S*L + VB4 + Wnd + Moon	16	466.6	0.0	0.164
30: Stat + Typ + Seas + Loc + VB4	12	466.9	0.3	0.141
32: Stat + Typ + Seas + Loc	11	467.3	0.8	0.113
26: Stat + Typ + Seas + Loc + S*L + VB4 + Wnd	15	467.6	1.1	0.096
27: Stat + Typ + Seas + Loc + S*L + VB4 + Moon	15	468.0	1.5	0.079
28: Stat + Typ + Seas + Loc + S*L + VB4	14	468.3	1.7	0.070
29: Stat + Typ + Seas + Loc + S*L	13	468.6	2.1	0.058
21: Stat + Typ + Seas + Loc + S*L + VB4 + Voc + Wnd + Moon	17	468.7	2.1	0.057
31: Stat + Typ + Seas + VB4	11	469.0	2.5	0.048
33: Stat + Typ + Seas	10	469.6	3.0	0.037
22: Stat + Typ + Seas + Loc + S*L + VB4 + Voc + Wnd	16	469.7	3.1	0.035
23: Stat + Typ + Seas + Loc + S*L + VB4 + Voc + Moon	16	470.0	3.5	0.029
25: Stat + Typ + Seas + Loc + S*L + VB4 + Voc	15	470.2	3.6	0.027
34: Stat + Typ	7	470.3	3.8	0.025
19: Stat + Typ + Seas + Loc + S*L + VB4 + Voc + Wnd + Moon + Sex	18	470.8	4.2	0.020

<sup>1</sup> Stat = Status, Typ = PB Type, Seas = Season, Loc = PB Location, S\*L = Status\*Location interaction,

VB4 = Vocals before PB, Voc = Vocal Response, Wnd = Wind.

Table 31. Parameters for confirmatory approach response analysis.

Parameter	Change in Logit or Logged Odds <sup>1</sup>				Odds Ratio <sup>1</sup>		
	$\tilde{\beta}$	$\hat{\beta}$	$\text{var}(\hat{\beta})$	90% CI <sup>2</sup>	$\tilde{\beta}$	$\hat{\beta}$	90% CI
Constant	-2.48	-2.48	0.49	-3.64 to -1.32	0.08	0.08	0.03 to 0.27
Beta	0.28	0.28	0.71	-1.10 to 1.66	1.32	1.32	0.33 to 5.26
Alpha	0.39	0.39	0.33	-0.56 to 1.34	1.48	1.48	0.57 to 3.84
PB inside home range	-0.10	-0.12	0.47	-1.23 to 1.03	0.90	0.89	0.29 to 2.79
Beta*PB inside HR	0.98	1.55	0.79	-0.48 to 2.44	2.67	4.69	0.62 to 11.52
Alpha*PB inside HR	0.59	0.92	0.51	-0.58 to 1.76	1.80	2.52	0.56 to 5.81
Siren PB	1.05	1.05	0.38	0.03 to 2.07	2.86	2.86	1.03 to 7.92
Human PB	1.07	1.07	0.26	0.23 to 1.91	2.92	2.92	1.26 to 6.77
Solo PB	0.16	0.16	0.34	-0.79 to 1.11	1.17	1.17	0.45 to 3.05
Group PB	1.26	1.26	0.30	0.36 to 2.16	3.53	3.53	1.43 to 8.68
Whelping season	0.06	0.06	0.12	-0.51 to 0.63	1.06	1.06	0.60 to 1.87
Rearing season	-0.50	-0.51	0.10	-1.02 to 0.02	0.61	0.60	0.36 to 1.02
Recovery season	-0.55	-0.57	0.12	-1.12 to 0.01	0.58	0.57	0.33 to 1.01
Vocals B4 playback	-0.68	-0.89	0.33	-1.63 to 0.26	0.50	0.41	0.20 to 1.30
High wind	-0.26	-0.69	0.16	-0.92 to 0.41	0.77	0.50	0.40 to 1.50
Moon up and bright	0.16	0.45	0.07	-0.28 to 0.60	1.17	1.57	0.76 to 1.81
Vocal Response	0.02	0.12	0.16	-0.64 to 0.68	1.02	1.13	0.53 to 1.98
Male	0.00	0.07	0.06	-0.41 to 0.41	1.00	1.08	0.66 to 1.51

<sup>1</sup> Change in logit of 0 or odds ratio of 1 indicates no difference between the parameter and reference group.

$$^2 \tilde{\beta} \pm 1.645 \sqrt{\text{var}(\hat{\beta})}.$$

Table 32. Final model set for exploratory approach response analysis.

Model <sup>1</sup>	K	AIC <sub>c</sub>	$\Delta_i$	$\omega_i$
40: Status + PB Type + Seas2 + Loc + T2b + VB4	11	437.1	0.0	0.165
62: Status + PB Type + Seas2 + Loc + T2b	10	437.3	0.3	0.145
41: Status + PB Type + Seas2 + Loc + T2b + VB4 + Wind	12	437.7	0.6	0.121
77: Status + PB Type + Seas2 + Loc + T2b + Wind	11	438.2	1.1	0.096
46: Status + PB Type + Seas2 + Loc + T2b + VB4 + NBPC	12	438.5	1.5	0.080
42: Status + PB Type + Seas2 + Loc + T2b + VB4 + Moon	12	438.7	1.6	0.073
65: Status + PB Type + Loc + T2b + VB4	10	438.9	1.9	0.065
71: Status + PB Type + Seas2 + Loc + T2b + VB4 + Wind + Moon	13	438.9	1.9	0.065
44: Status + PB Type + Seas2 + Loc + T2b + VB4 + Sex	12	439.0	1.9	0.065
80: Status + PB Type + Seas2 + Loc + T2b + NBPC	11	439.0	1.9	0.063
63: Status + PB Type + Seas2 + Loc + VB4	10	439.1	2.0	0.062

<sup>1</sup> Seas2 = Season with 2 categories (1 Jan to 15 June, 16 June to 31 Dec), Loc = PB location, T2b = PB

time with 2 categories (after sunrise and earlier), VB4 = Vocals before PB, NBPC = Net barometric pressure change.

Table 33. Parameters for exploratory approach response analysis.

Parameter	Change in Logit or Logged Odds <sup>1</sup>				Odds Ratio <sup>1</sup>		
	$\hat{\beta}$	$\hat{\beta}$	$\text{var}(\hat{\beta})$	90% CI <sup>2</sup>	$\hat{\beta}$	$\hat{\beta}$	90% CI
Constant	-2.80	-2.80	0.37	-3.81 to -1.80	0.06	0.06	0.02 to 0.16
Beta	0.96	0.96	0.16	0.29 to 1.62	2.60	2.60	1.34 to 5.04
Alpha	0.89	0.89	0.12	0.33 to 1.46	2.44	2.44	1.39 to 4.29
Siren PB	0.95	0.95	0.38	-0.06 to 1.97	2.59	2.59	0.93 to 7.19
Human PB	1.05	1.05	0.27	0.19 to 1.91	2.85	2.85	1.21 to 6.72
Solo PB	0.01	0.01	0.35	-0.96 to 0.98	1.01	1.01	0.38 to 2.67
Group PB	1.22	1.22	0.31	0.31 to 2.13	3.39	3.39	1.36 to 8.44
PB inside home range	0.59	0.59	0.07	0.15 to 1.04	1.81	1.81	1.16 to 2.82
16 Jun to 31 Dec	-0.48	-0.52	0.07	-0.91 to -0.06	0.62	0.60	0.40 to 0.94
PB after sunrise	-0.58	-0.62	0.11	-1.11 to -0.04	0.56	0.54	0.33 to 0.96
Vocals B4 playback	-0.58	-0.84	0.32	-1.52 to 0.35	0.56	0.43	0.22 to 1.42
High wind	-0.13	-0.47	0.16	-0.79 to 0.53	0.88	0.62	0.45 to 1.69
Moon up and bright	0.03	0.22	0.07	-0.41 to 0.47	1.03	1.24	0.66 to 1.60
Male	0.01	0.12	0.06	-0.40 to 0.42	1.01	1.13	0.67 to 1.52
1 mbar net baro change <sup>3</sup>	-0.01	-0.07	0.01	-0.16 to 0.14	0.99	0.93	0.85 to 1.15
3 mbar net baro change <sup>3</sup>	-0.03	-0.21	0.03	-0.29 to 0.23	0.97	0.81	0.75 to 1.26

<sup>1</sup> Change in logit of 0 or odds ratio of 1 indicates no difference between the parameter and reference group.

$$^2 \hat{\beta} \pm 1.645 \sqrt{\text{var}(\hat{\beta})}.$$

<sup>3</sup> Net barometric pressure change data ranges from -2.7 to +6.1 millibars.

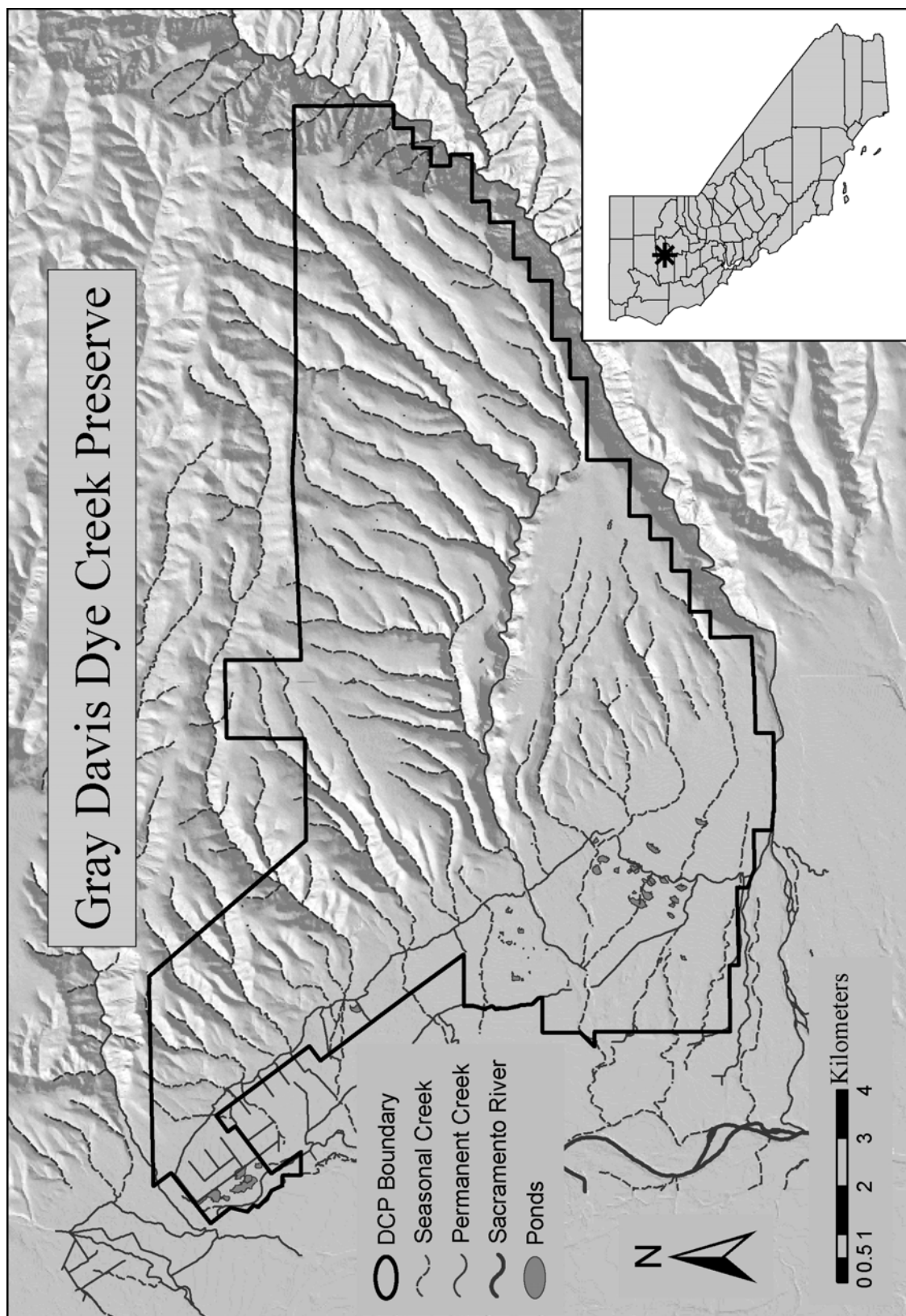


Figure 15. Dye Creek Preserve area.

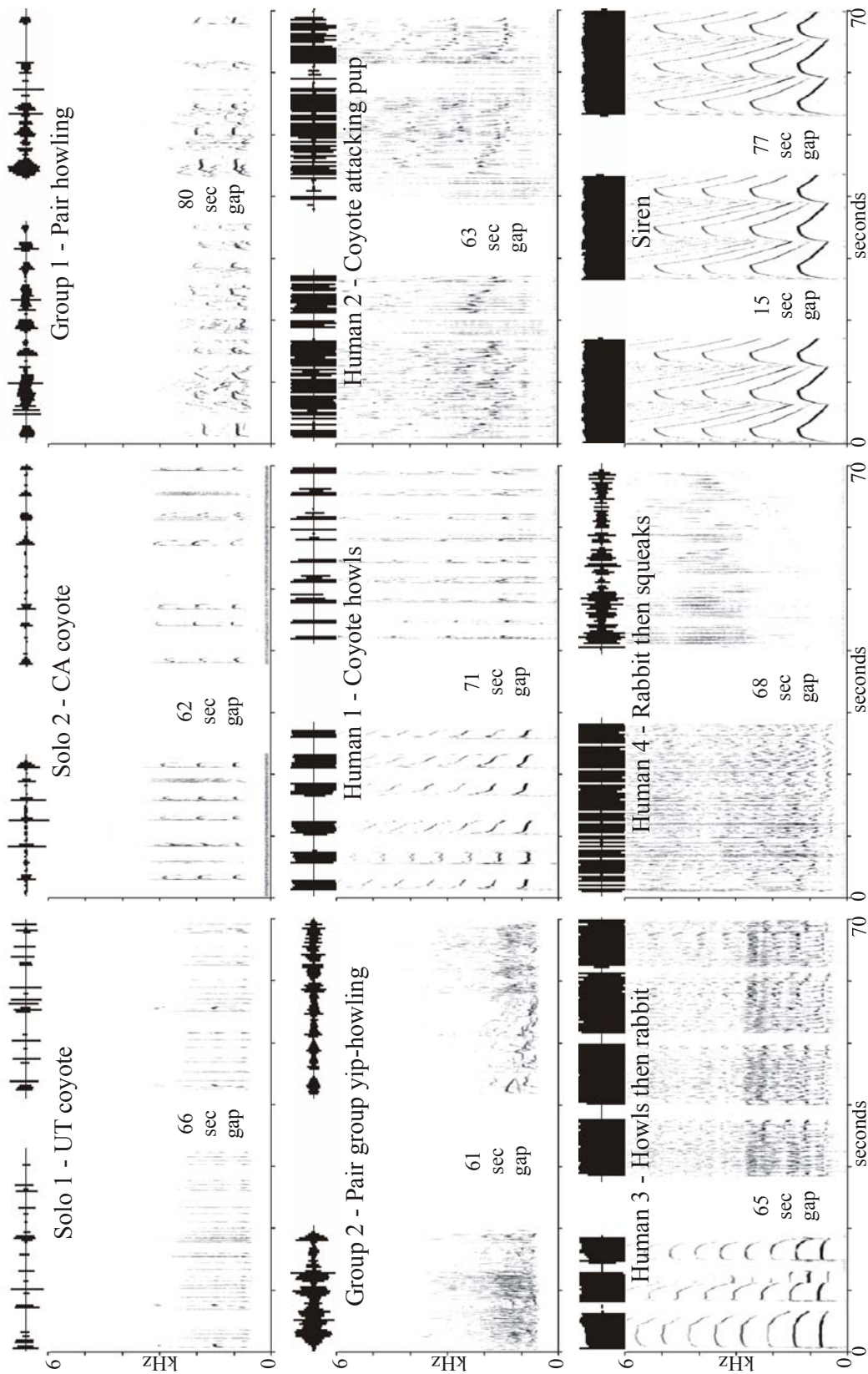


Figure 16. Audio stimuli for playback trials. Upper graph in each pane is relative sound amplitude over time, lower graph is sound spectrogram (frequency of sound energy over time). Duration of silence between playback segments is noted.

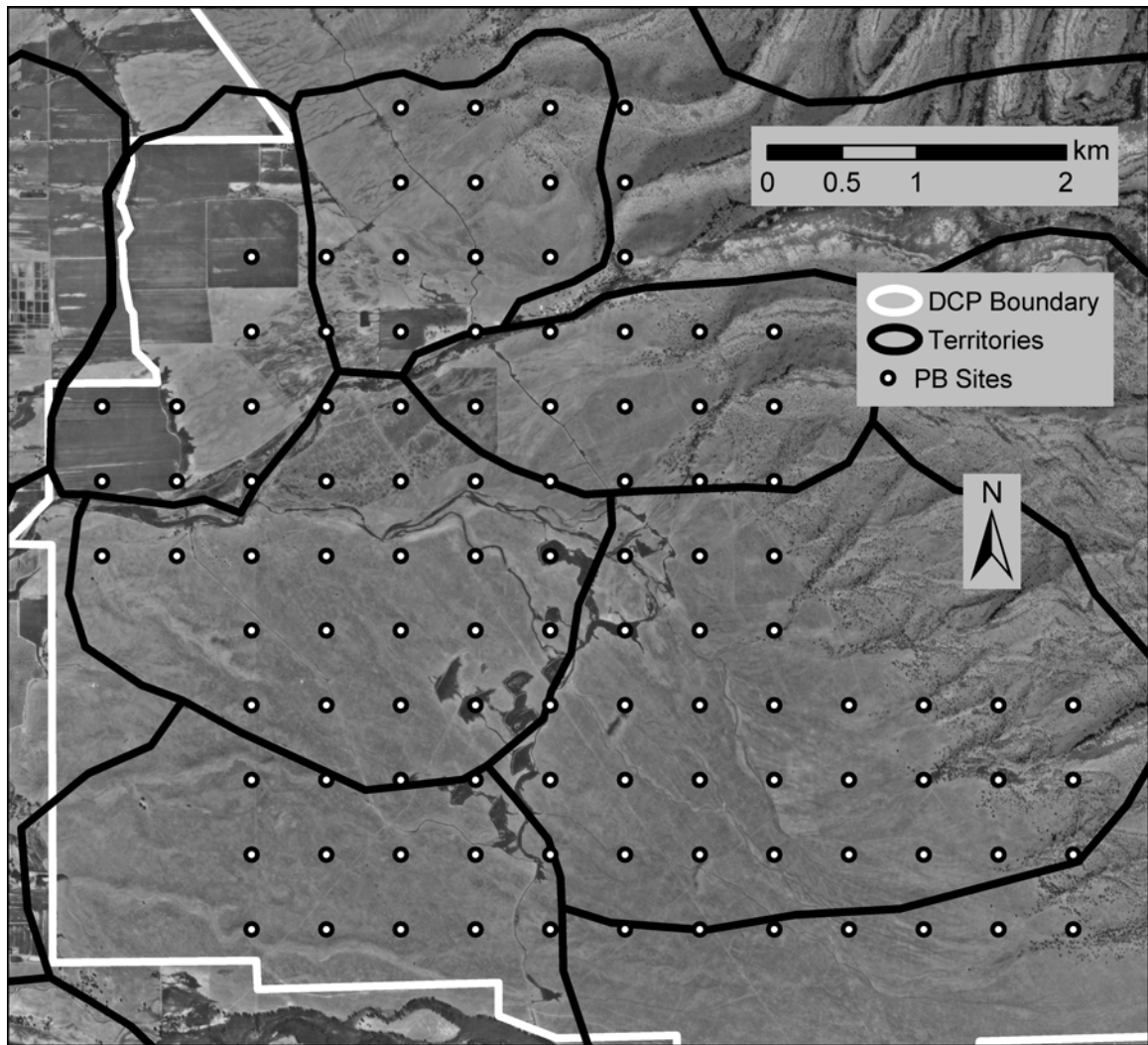


Figure 17. Playback sites and coyote territories on the southwestern portion of the DCP.

The background is a combination of aerial photography and hill shading to show habitat and topography.

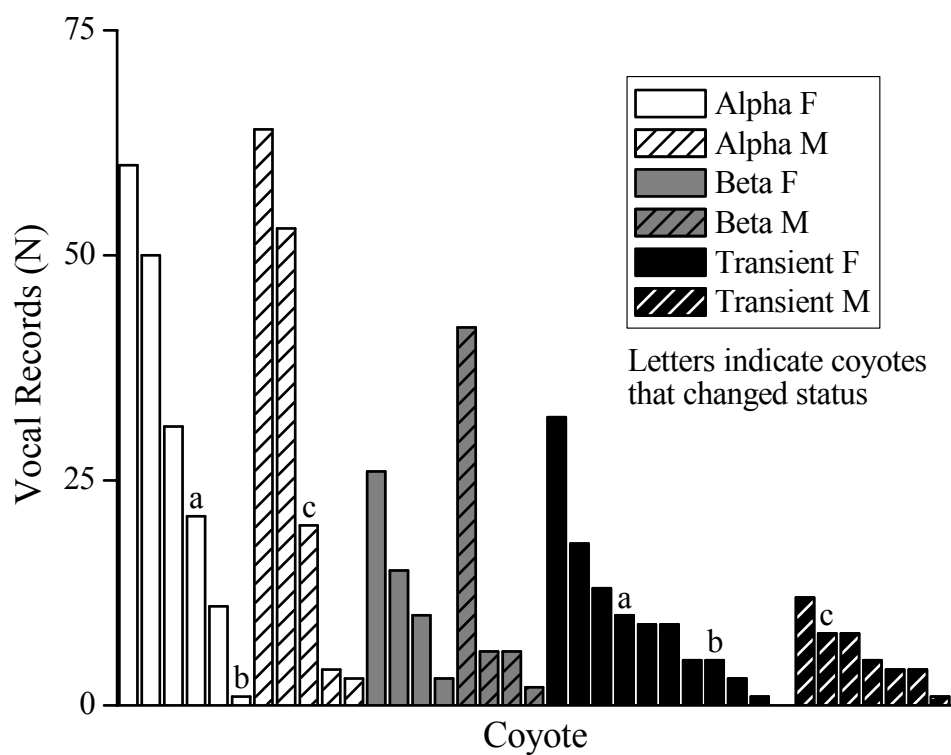


Figure 18. Number of records per coyote in the vocal response data set.

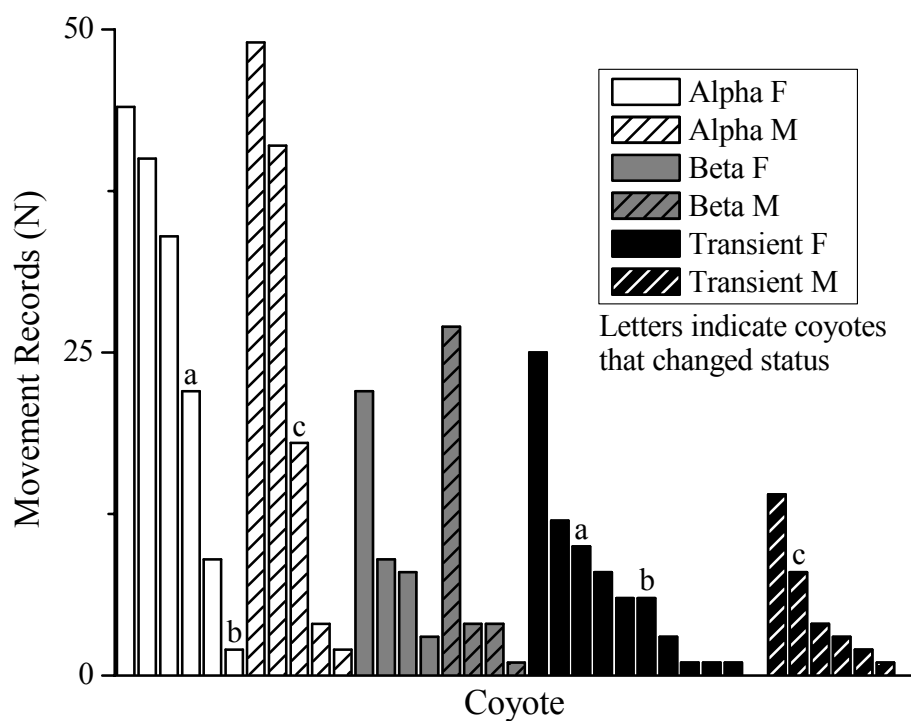


Figure 19. Number of records per coyote in the approach response data set.



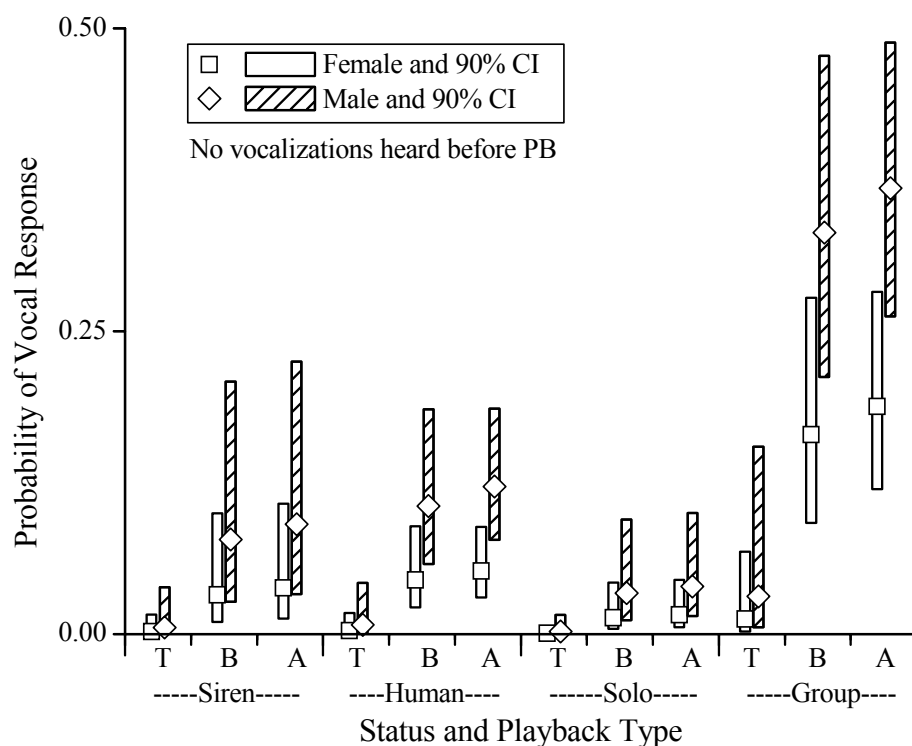


Figure 20. Probability of vocal response estimated from confirmatory analysis results.

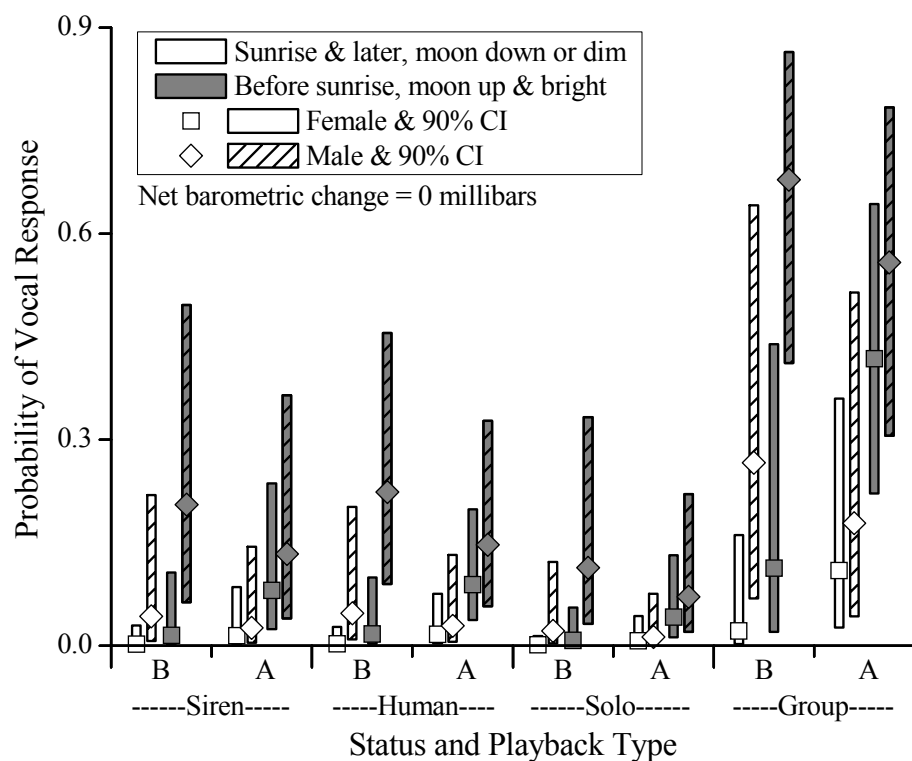


Figure 21. Probability of vocal response estimated from exploratory analysis results.

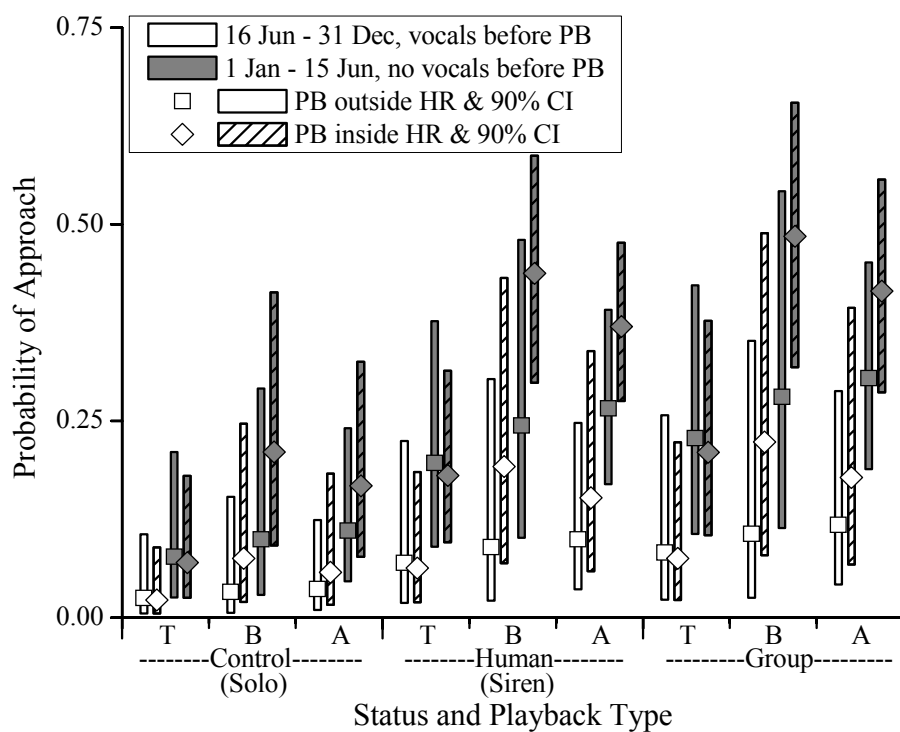


Figure 22. Probability of approach estimated from confirmatory analysis results.

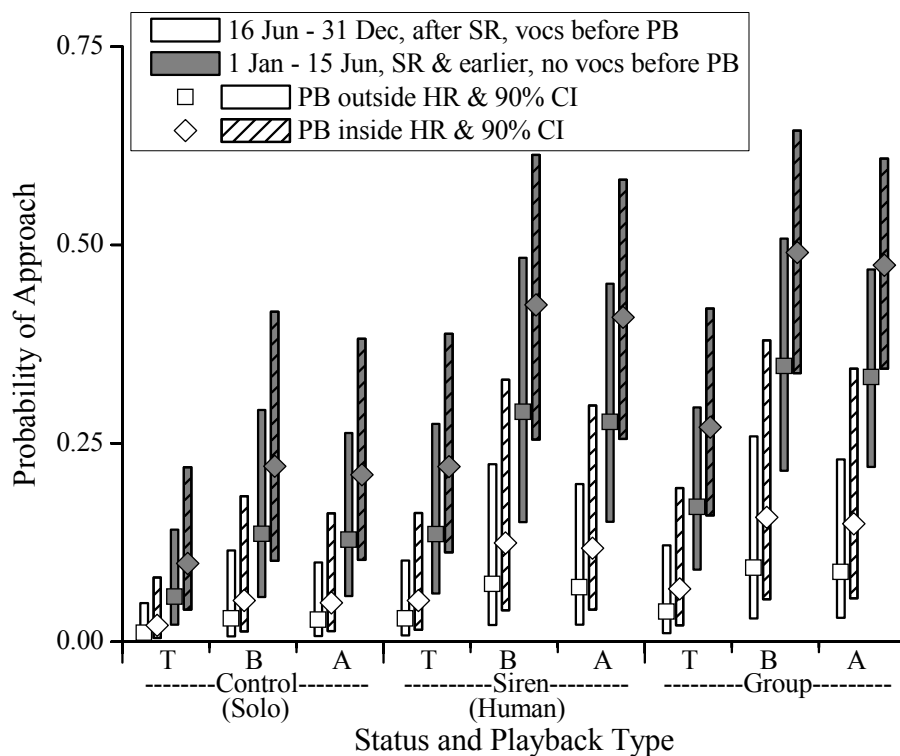


Figure 23. Probability of approach estimated from exploratory analysis results.

## **APPENDIX 1. SEX-BASED DIFFERENCES IN COYOTE VOCALIZATIONS**

### **INTRODUCTION**

Many species have a sexual dimorphism in the type and frequency of their vocalizations. Male elk are the only ones to bugle (Nowak 1999: 1111), male songbirds usually sing more elaborately and frequently (Ehrlich et al. 1988: 471-475), and only male frogs vocalize (Emerson 2001). These differences are generally tied to reproductive roles; males often have to defend females or a breeding territory, or they must advertise to attract mates.

Even if both sexes of a species share call types and frequencies, there may be sexually specific cues within the vocalizations that allow listeners to determine the calling individual's sex. Sexual differences could arise from physiological disparities in sexually dimorphic species (Ballintijn and Ten Cate 1997, Bachorowski and Owren 1999), and receivers could use these cues to decide on an appropriate course of action (e.g., confront individuals of the same sex and court the opposite sex). Sexual differences have been reported in the vocalizations of birds (Ballintijn and Ten Cate 1997), primates (Mitani and Gros-Louis 1995, Weiss et al. 2001), and ungulates (Reby et al. 1999). A few studies with passerine birds have also demonstrated behavioral discrimination between male and female vocalizations (Okanoya and Kimura 1993, Vicario et al. 2001).

I am unaware of any research documenting sexual differences in coyote vocalizations, although differences should be expected based on the alpha male's lead role in territory defense (Gese 2001). I used 4 captive pairs of coyotes (Chapter 2) to investigate whether male and female coyotes bark or howl at different rates. I also examined whether there were sex-based differences in the characteristics of their

vocalizations. I predicted that males would be more vocal than females, and that there would be signs of sex-based differences in their vocalizations.

## **METHODS**

I recorded vocalizations from 4 pairs of captive coyotes (Chapter 2), and investigated differences in male and female vocalization rates by tabulating the following for each individual: recording duration, number of solo barks, number of barks, number of solo howls, and number of howls. A “solo” vocalization was one that was not overlapped by a vocalization from the animal’s mate, and vocalizations were only used if I was able to identify the individual producing the sound. I converted each number of vocalizations into a rate (vocalizations per hour of recording time). Vocalization rates of males and females were tested for unequal variances and then compared using t-tests in JMP IN 4.0 (SAS Institute, Cary, North Carolina, USA). Because the 4 vocalization rates were related information, I applied a Bonferroni adjustment to the usual 0.05 significance level, resulting in a significance level of 0.0125.

I used linear discriminant analysis to classify barks and howls to the sex of the individual producing them. Variables and statistical procedures were identical to those described in Chapter 2. These analyses were pseudoreplicated; there were many cases but only 5 (for barks) or 6 (for howls) individuals involved. Because they lacked true replication, the results could only indicate that sex-based differences were possible, not that they occurred.

## **RESULTS**

### **Vocalization Rates**

There was a great deal of inter-individual variability in bark rates, and considerably less variability in howl rates (Table 34). This translated to no difference between males and females in total or solo bark rates, a significant difference between the sexes in solo howl rates, and a trend towards a sex difference in total howl rates (Table 35). Females rarely howled when their mates were not vocalizing; their solo howl rate was only 20% of the male solo howling rate. In addition, the female that was most likely to howl by herself howled at less than 60% the rate of the male with the lowest howling rate. These results suggest that females let their mate take the lead in howling bouts, and that they time their howls to overlap with the male's barks and howls. The trend towards a lower total female howling rate was probably due to the reticence of females to howl by themselves, because in both sexes the total howl rate minus the solo howl rate was about 2.75 howls per hour.

Out of 100 recorded vocalization bouts, males initiated 61 bouts, females began 6 bouts, and the pair began barking or howling at approximately the same time in 33 cases. Fifty-three of these bouts were concluded by the male, while 22 were finished by the female.

### **Bark Discriminant Analysis**

The evidence in the raw data for true sex-based differences was weak (Table 3), because the measurements for individual males (M-5320, M-5416, and M-5429) generally overlapped those for individual females (F-5438 and F-5471). The exception was the harmonic-to-noise ratio (HNR), where females had higher mean values than

males, indicating that males had noisier (i.e. rougher or more chaotic) barks. ANOVAs using the individual means with sex as the model effect were not significant (Bonferroni-corrected  $\alpha = 0.005$ ) for any of the bark variables; all probabilities exceeded 0.15.

Both forwards and backwards stepwise discriminant analysis converged on a model containing 4 variables: maximum dB, standard deviation, kurtosis, and HNR. The squared canonical correlation for the resulting discriminant function was 0.33, which meant that sex explained 33% of the variation in the value of the discriminant function for each bark. The discriminant function had statistically significant discriminatory power ( $F_{4, 214} = 26.4$ ,  $p < 0.0001$ ). The absolute values of the standardized coefficients reflected each variable's relative importance in the discriminant function; in this case maximum dB level was the most important variable, with a coefficient of 0.88. The other variables were also somewhat important, with coefficient absolute values between 0.50 and 0.68. Females were louder, with a higher standard deviation, lower kurtosis, and higher HNR than males. The discriminant function classified 80% of 219 training barks correctly, with errors evenly split between males and females. The test data were classified with a similar accuracy – 81% of 74 barks, but in this case female barks were more often classified correctly (94%) than male barks (72%). Kappa was  $0.59 \pm 0.11$  ( $\bar{x} \pm 95\% \text{ CI}$ ) for the training data and  $0.63 \pm 0.18$  for the test data, so the discriminant model gave a 60% improvement over chance classification. The large change in percentage accuracy for each sex between training and test data sets suggests that the discriminant model may have been biased toward characteristics of certain individuals due to pseudoreplication.

### **Howl Discriminant Analysis**

There was no solid evidence of sex-based differences in the raw howl data (Table 8), since mean values for the 4 males (M-5320, M-5416, M-5429, and M-5430) generally overlapped the values for the 2 females (F-5414 and F-5438). Females did have higher mean start frequencies than the males did, and they had fewer irregularities in the rising portion of their howls. ANOVAs using the individual means with sex as the model effect were not significant (Bonferroni-corrected  $\alpha = 0.002$ ) for any of the howl variables; all probabilities were greater than 0.20, except for start frequency ( $p = 0.08$ ) and rise irregularities ( $p = 0.15$ ).

Both forwards and backwards stepwise procedures converged on the same model for classifying howls based on sex. The final model contained 7 variables: all frequency measurements except the end frequency, the number of nonlinearities in the rise and fall, and the number of 50-Hz to 100-Hz wavers in the middle section of the howl. The resulting discriminant function was statistically significant ( $F_{7, 201} = 8.73$ ,  $p < 0.0001$ ) and the squared canonical correlation of 0.233 meant that sex explained approximately 25% of the variation in the value of the discriminant function for each howl. The standardized coefficients indicated that the maximum frequency was most important (coefficient of 1.65), and that the remaining frequency measurements were less than half as important (coefficient absolute values between 0.61 and 0.80). Nonlinear phenomena and wavers were less useful for classifying howls to sex (coefficients between 0.24 and 0.36). Females had higher start, end of rise, and start of fall frequencies than males, and lower maximum frequencies. Females also had fewer irregularities and wavers in their howls than males. The coefficients for the end of rise, maximum, and start of fall frequencies

were somewhat problematic, because the actual values for the 2 individual females were always higher than those for M-5429 and M-5430, and always lower than those for M-5320 and M-5416 (Table 8). The discriminant function apparently homed in on differences that arose by chance through the pseudo-replicated nature of this analysis and the differing sample sizes for each individual.

Nevertheless, the discriminant function classified 77% of 209 howls to the correct sex, with errors twice more likely for male than for female howls. The test data were also correctly classified 77% of the time, and this time error rates were the same for male and female howls. The kappa estimates were  $0.41 \pm 0.15$  ( $\bar{x} \pm 95\%$  CI) for the training data and  $0.37 \pm 0.27$  for the test data, so this model represented a moderate improvement over chance classification.

## **DISCUSSION**

### **Sexual Differences in Howling Rates**

The most striking sex-based difference in coyote barks and howls was the reticence of female coyotes to howl when their mates were not vocalizing. Almost all of the recorded vocalization sequences were in direct response to vocalizations from other coyotes at the NWRC facility, so the communicative situation was presumably agonistic and related to declaring “territorial” occupancy. Males were clearly much more likely to initiate bouts than females were, and they tended to vocalize for longer periods of time. In addition, 10 bouts contained only male vocalizations and none of the sequences consisted entirely of female barks and howls.

These results suggest that male coyotes are likely to take the lead in territorial disputes, just as they take the lead during cooperative hunts (Gese and Grothe 1995).



Vocal territory defense led by male coyotes certainly matches the pattern observed by hunters who use coyote vocalizations and dogs to attract coyotes; this hunting method killed 4 males for every female in a population with an approximately equal sex ratio (Wagner 1997). Although Gese and Ruff (1998) did not find a sex bias in the vocalization rates of coyotes in their study, they did not report which animal began or finished howling bouts.

Wolves also appear to follow a pattern of males taking the lead in howling and territory defense. Tooze et al. (1990) did not report the vocalization rates of their 7 captive study animals, but their sample sizes indicated that isolated females howled less than isolated males: they recorded between 8 and 50 howls from 4 females, and 56 to 60 howls from 3 males. Harrington and Mech (1979) found that alpha males were most responsive to playbacks, and that when they responded they tended to howl longer than other wolves.

### **Sexually Specific Cues in Coyote Vocalizations**

Discriminant analysis classified barks to the appropriate sex 80% of the time (a 59% chance-corrected accuracy). While this result seems promising, the low number of individuals (3 males and 2 females) used in the analysis casts doubt on the finding of sex-based differences. Individual differences and unequal sample sizes likely contributed to classification accuracy. HNR was the only variable used in the discriminant function in which the individual female means were not overlapped by individual male means, but even in this case actual HNR values overlapped considerably – apart from 1 female bark with an HNR of 35 volts, all 5 individuals produced barks with HNRs from 2 to 19 volts.

Classification of howls to the correct sex was slightly less accurate than barks, and this result is also suspect because of pseudoreplication. There were, nevertheless, some hints of sex-based differences. Howl start frequency differed between males and females: 76% of male howls started below 400 Hz and only 33% of female howls began below this level. The lowest fundamental frequency that animals can produce is related to features that scale with body size, and it is possible that smaller female coyotes find it more difficult to start their howls at the low frequencies used by males.

The other important sex-based difference was the tendency of male howls to contain more nonlinearities than female howls. Only 48% of female howls contained 1 or more subharmonic or chaotic sections, while 72% of male howls had at least 1 of these nonlinear features. There has been a recent surge of interest in the possible adaptive significance of nonlinear phenomena in vocalizations, but these features are still poorly understood (Fitch et al. 2002). The sex-based differences seen in coyote howl nonlinearities could stem from physiology, provided that individuals with larger larynxes and vocal folds have a lower threshold for producing these sounds. It is also possible that nonlinearities, which typically sound harsh to listeners, function in an agonistic context and signal higher levels of aggression in males.

The results therefore suggest that certain features of coyote vocalizations may predominate in one sex or the other. These findings need to be verified with data recorded from a larger number of individuals.

Table 34. Vocalization data for coyotes at the NWRC Logan Field Station, July 1998.

Coyote	Hours Recorded	Solo Barks	Total Barks	Solo Howls	Total Howls
F-5414	18.22	4	11	26	123
F-5415	17.00	1	1	3	49
F-5438	20.17	45	58	19	58
F-5471	16.75	270	356	9	24
M-5320	18.22	287	314	62	139
M-5416	16.75	78	146	67	100
M-5429	20.17	65	70	42	89
M-5430	17.00	34	36	95	139

Table 35. Vocalization rates (vocalizations per hour) for coyotes at the NWRC Logan Field Station, July 1998.

Comparison	Male Mean $\pm$ SE <sup>1</sup>	Female Mean $\pm$ SE <sup>1</sup>	t <sub>DF=6</sub>	p(t) <sup>2</sup>
Solo Bark Rate	6.408 $\pm$ 3.162	4.657 $\pm$ 3.853	0.351	0.7374
Total Bark Rate	7.885 $\pm$ 3.426	6.198 $\pm$ 5.056	0.276	0.7917
Solo Howl Rate	3.768 $\pm$ 1.454	0.771 $\pm$ 0.538	3.867	0.0083*
Total Howl Rate	6.547 $\pm$ 0.852	3.485 $\pm$ 1.141	2.150	0.0751

<sup>1</sup> n = 4 males and 4 females<sup>2</sup>  $\alpha$  equals 0.0125

## **APPENDIX 2. TESTING INDEPENDENCE OF BARK AND HOWL MEASUREMENTS**

My recorded bark and howl data sets included numerous cases of temporally close vocalizations, and these cases violated the discriminant analysis assumption of statistical independence to the extent that adjacent vocalizations from an individual were temporally autocorrelated.

For a given variable, autocorrelation was present if the variance of the difference in values between adjacent vocalizations was lower than the variance of the difference in values between randomly paired vocalizations. I tested for the presence of temporal autocorrelation by selecting individuals with more than 75 barks (2 individuals) or 50 howls (3 individuals). I looked for barks within 1 second of each other or howls within 30 seconds of each other, and calculated the difference in the value of each variable between the adjacent vocalizations. If vocalizations were part of a series (i.e., 3 or more barks in a row that were within 1 second of the previous bark), then I did not use the same vocalization in multiple calculations. I also matched the first vocalization of each adjacent pair with a randomly selected vocalization, and calculated the difference in the value of each variable between these randomly paired vocalizations. I used JMP IN 4.0's O'Brien test (SAS Institute, Cary, North Carolina, USA) to check for differences between variances computed on adjacent and randomly paired vocalizations. I used a Bonferroni-corrected significance level of  $0.05/n$  for each individual's data, where  $n$  equaled the number of variables tested.

The evidence for temporal autocorrelation of bark characteristics was weak (Table 36). Although the harmonic-to-noise ratio (HNR) showed statistically significant

autocorrelation for coyote F-5471, no other comparison showed a significantly lower variance for adjacent barks when compared to randomly paired barks. However, 9 of 11 comparisons for coyote M-5320 and 10 of 11 comparisons for F-5471 had lower measured variances for adjacent barks. This pervasive, although not statistically significant, trend indicates that there was probably a small amount of temporal autocorrelation in bark characteristics. This translates into a slight violation of the assumption of independence.

There was even less evidence for temporal autocorrelation of howl characteristics (Table 37). The only comparison that approached statistical significance was the maximum to start of fall duration for coyote M-5430. In addition, only 14 of 23 comparisons for M-5320, 15 of 24 comparisons for M-5416, and 17 of 26 comparisons for M-5430 showed trends towards lower variance for adjacent howls. There was no evidence for temporal autocorrelation, so it is unlikely that statistical independence was violated by using adjacent howls by the same individual.

Table 36. Temporal autocorrelation of bark variables according to the O'Brien F-test for unequal variances.

Variable	M-5320 (N = 15 barks)				F-5471 (N =19 barks)			
	Adjacent Standard Deviation	Random Standard Deviation	$F_{1,28}$	$p(F)^1$	Adjacent Standard Deviation	Random Standard Deviation	$F_{1,36}$	$p(F)^1$
Duration (ms)	11.25	13.54	0.345	0.5619	10.76	11.04	0.004	0.9472
Bark Structure	0.640	0.834	1.767	0.1945	0.602	1.01	3.451	0.0714
Bark Harmonic Structure	1.62	2.47	2.772	0.1071	1.03	1.72	2.578	0.1171
Max dB (dB-volts)	5.39	6.40	0.494	0.4880	2.46	7.08	5.463	0.0251
Max dB Frequency (Hz)	174.28	152.80	0.077	0.7840	31.27	39.59	0.817	0.3721
Mean (Hz)	57.39	116.05	5.308	0.0289	63.00	101.67	3.392	0.0738
Standard Deviation (Hz)	61.03	65.37	0.127	0.7241	43.46	101.80	3.900	0.0560
Skewness	0.304	0.682	6.735	0.0149	0.208	0.301	1.612	0.2124
Kurtosis	1.77	2.77	3.185	0.0851	0.723	0.826	0.289	0.5940
HNR (volts)	4.63	6.70	3.353	0.0778	2.38	4.67	10.378	0.0027*
HNR Frequency (Hz)	405.60	377.62	0.015	0.9039	43.06	39.87	0.081	0.7775

<sup>1</sup>  $\alpha$  equals 0.0045

Table 37. Temporal autocorrelation of howl variables according to the O'Brien F-test for unequal variances.

Variable	M-5320 (N = 13 howls)				M-5416 ( N = 20 howls)				M-5430 (N = 33 howls)			
	Adjacent Standard Deviation	Random Standard Deviation	F <sub>1, 24</sub>	p(F) <sup>1</sup>	Adjacent Standard Deviation	Random Standard Deviation	F <sub>1, 38</sub>	p(F) <sup>1</sup>	Adjacent Standard Deviation	Random Standard Deviation	F <sub>1, 64</sub>	p(F) <sup>1</sup>
Start Frequency (Hz)	46.1	64.6	1.320	0.2619	32.4	55.0	4.185	0.0478	38.5	87.3	2.450	0.1224
End Rise Freq (Hz)	156.2	114.5	1.435	0.2426	238.6	291.4	0.535	0.4689	190.8	294.4	3.012	0.0875
Maximum Freq (Hz)	197.8	155.8	0.673	0.4200	130.0	129.8	0.000	0.9975	114.9	209.0	1.079	0.3028
Start Fall Freq (Hz)	387.0	338.5	0.164	0.6894	141.2	146.1	0.007	0.9356	156.8	234.6	1.701	0.1969
End Frequency (Hz)	499.8	413.9	0.546	0.4673	72.0	112.7	4.762	0.0353	87.9	135.4	0.954	0.3325
Rise Duration (ms)	128.3	151.4	0.505	0.4841	161.2	168.0	0.032	0.8594	121.3	125.4	0.030	0.8637
End Rise to Max Duration (ms)	842.8	1061.0	0.429	0.5187	230.4	272.6	1.253	0.2701	318.7	358.0	0.224	0.6377
Max to Start Fall Duration (ms)	899.3	1174.5	1.029	0.3205	493.9	731.1	2.606	0.1147	295.9	497.4	10.205	0.0022
Fall Duration (ms)	103.9	105.5	0.001	0.9777	65.8	40.0	0.536	0.4686	53.1	56.4	0.084	0.7731
Rise Slope (Hz/ms)	2.46	3.42	1.183	0.2876	0.87	1.30	2.377	0.1315	1.12	1.48	2.05	0.1570
End Rise to Max Slope (Hz/ms)	0.443	0.462	0.024	0.8790	0.553	0.347	2.118	0.1538	0.657	0.718	0.118	0.7325
Max to Start Fall Slope (Hz/ms)	0.473	0.624	0.538	0.4703	0.358	0.247	0.625	0.4340	0.717	0.680	0.061	0.8065
Fall Slope (Hz/ms)	4.22	3.59	0.202	0.6573	3.69	4.03	0.157	0.6939	3.43	3.46	0.004	0.9491
Rise Nonlinearity	0.707	0.641	0.157	0.6953	0.523	0.768	3.995	0.0528	0.728	0.712	0.020	0.8881

<sup>1</sup>  $\alpha$  equals 0.0022 for M-5320, 0.0021 for M-5416, and 0.0019 for M-5430

Table 37. Continued.

Variable	M-5320 (N = 13 howls)				M-5416 (N = 20 howls)				M-5430 (N = 33 howls)			
	Adjacent Standard Deviation	Random Standard Deviation	$F_{1,24}$	$p(F)^1$	Adjacent Standard Deviation	Random Standard Deviation	$F_{1,38}$	$p(F)^1$	Adjacent Standard Deviation	Random Standard Deviation	$F_{1,64}$	$p(F)^1$
Middle Nonlinearity	0.00	0.00	N/A	N/A	0.224	0.224	0.000	1.0000	1.33	1.55	0.461	0.4994
Fall Nonlinearity	0.00	0.00	N/A	N/A	0.00	0.00	N/A	N/A	0.384	0.354	0.071	0.7906
50 to 100 Hz Freq Shifts	0.00	0.00	N/A	N/A	0.447	0.324	0.207	0.6521	0.500	0.394	0.388	0.5355
100+ Hz Freq Shifts	0.76	1.12	1.095	0.3057	0.394	0.394	0.000	1.0000	0.650	0.707	0.118	0.7322
0 to 50 Hz Rise Wavers	0.801	0.641	0.442	0.5124	0.725	1.021	0.829	0.3683	0.781	0.585	1.52	0.2216
50 to 100 Hz Rise Wavers	0.725	0.555	0.480	0.4949	0.394	0.000	3.248	0.0794	0.384	0.467	0.530	0.4695
100 to 200 Hz Rise Wavers	0.408	0.494	0.188	0.6687	0.489	0.394	0.441	0.5106	0.242	0.000	2.28	0.1356
200+ Hz Rise Wavers	0.277	0.494	1.206	0.2830	0.366	0.553	1.855	0.1812	0.174	0.000	1.03	0.3135
50 to 100 Hz Middle Wavers	2.14	2.17	0.001	0.9770	0.394	0.447	0.127	0.7237	1.05	1.43	2.41	0.1251
100 to 200 Hz Middle Wavers	0.408	0.277	0.416	0.5249	0.00	0.00	N/A	N/A	1.27	0.97	1.62	0.2071
200+ Hz Middle Wavers	0.277	0.408	0.416	0.5249	0.447	0.510	0.044	0.8342	0.433	0.394	0.031	0.8612
Body Shape	2.29	2.50	0.150	0.7017	2.04	2.39	0.768	0.3864	1.80	2.46	3.98	0.0504

<sup>1</sup>  $\alpha$  equals 0.0022 for M-5320, 0.0021 for M-5416, and 0.0019 for M-5430



### **APPENDIX 3. DISTANCE AND INTERACTION EFFECTS IN THE BARK VARIABLE MANOVAS**

The pervasive presence of interaction effects in the bark variable repeated measures MANOVAs was troubling. Potential causes included sound processing and playback effects, measurement error, and the non-random presentation of each individual's vocalizations during field playbacks. Presentation was non-random because vocalizations were played in the order they were recorded, and each individual's vocalizations were grouped on 2 or 3 sections of the playback.

#### **RECORDING CONDITIONS**

One cause of the interaction effects could be related to the non-random presentation of each individual's vocalizations during field playbacks, coupled with changes in recording conditions over the course of the 50-min playbacks. Some individuals' vocalizations were predominantly in the first half of the playback during the best recording conditions, while others were predominantly in the second half of the playback, when conditions were worse.

I compared signal-to-noise ratio (SNR) values (which estimated recording quality) with the other variables at all distances. The absolute value of the correlation between SNR and the other bark variables was always below 0.35, except that SNR at 1,000 meters had a -0.52 correlation with standard deviation. With only the single exception, SNR never explained more than 12% of the variation in measurements. However, SNR did not need to correlate with variables at a given distance to have an effect on variables across different distances. SNR could still be important if the difference in SNR between 2 distances correlated with the difference in other variables

between the same distances. I calculated the change in SNR and the other bark variables between the 10-m and 500-m, 10-m and 1,000-m, and 500-m and 1,000-m distances, and looked for correlations. The absolute values of all correlations were below 0.35, with the exception of standard deviation (-0.42 between 10-m and 1,000-m, and -0.57 between 500-m and 1,000-m). At best, then, SNR explained less than a third of the variation in how measurements changed between distances, and it almost always explained less than 12% of this variation.

I also checked to see if the amount of low-frequency noise (used to generate SNR, and indicative of wind speed and airplane noise) explained some of the interaction effects. The absolute value of the correlation between the amount of low frequency noise and the other variables was always below 0.30. Similarly, the change in low frequency noise between the different distances was never correlated with changes in other variables between the same distances – the absolute values of the correlations were always below 0.20. Estimates of recording quality therefore did not explain the interaction effects in the MANOVAs.

## **DISTANCE AND INTERACTION EFFECTS**

Other possible explanations for the interactions included the influence of sample size variability, sound processing and playback effects, and various types of measurement error. Examining the graphs of how individual means changed with distance helped to explain some of the interaction effects as well as some of the distance effects seen in the MANOVAs.

*Bark Duration.*--There was no significant interaction effect for bark duration, and the distance effect was primarily due to an increase in duration between the noise-reduced

and 10-m distances (Figure 24). This jump was apparently an artifact of the playback equipment used, since it was relatively uniform between the different individuals.

Otherwise there appeared to be a slight decrease in duration due to noise reduction, and a tendency for duration to decrease from 10-m to 1,000-m.

*Bark Structure and Bark Harmonic Structure.*--Bark structure increased at the noise-reduced distance (Figure 8), which is not surprising since noise reduction probably removed background noise that was making harmonics more difficult to see. Bark structure then tended to decrease with increasing distance, as background noise increased due to playback and sound transmission. M-5429's barks are steady at a bark structure of approximately 1 (corresponding to noisy barks) beyond the noise-reduced distance; his bark structure did not decrease because it was at the minimum value. M-5416 and F-5471 showed a sharp dip at 500-m. These animals were a mated pair, and so their barks were evaluated at the same time. The raw data showed a region of depressed bark structure values, and spot-checking several of the barks indicated that these vocalizations were scored lower than they should have been.

Bark harmonic structure showed the same general pattern at different distances as bark structure, for similar reasons (Figure 25). Harmonic structure should have increased at the noise-reduced distance if noise reduction allowed harmonics to be seen in barks that were classified as "noisy" (a value of 1) at the initial distance. Then, as the barks were played back and re-recorded at increasing distance, the playback speakers and sound transmission tended to add more noise, which decreased harmonic structure and led to more barks being rated "noisy". M-5416 and F-5471 showed the same dip at

500-m as was seen for bark structure; bark structure and bark harmonic structure were estimated at the same time.

*Maximum dB.*--Maximum dB level was expected to increase dramatically at the second distance, due to sound amplitude normalization, and then decrease by about 6 dB for every doubling of distance from playback (Naguib and Wiley 2001). This was almost exactly the pattern seen (Figure 26), except that the overall decrease in maximum dB between 500-m and 1,000-m was only 3.3 dB-volts. In addition, M-5320 showed a much sharper drop in max dB than the other individuals. Atmospheric turbulence and temperature and velocity gradients are known to affect sound amplitude (Naguib and Wiley 2001), and differences in these factors within and between recording sessions may explain the unusual features of the measurements.

*Maximum dB Frequency.*--Maximum dB frequency was not affected by noise reduction and normalization, but it was increased by playback (Figure 27). This increase was apparently due to an overemphasis of higher frequencies by the speaker. The prominent dip in maximum dB frequency at 500-m is hard to explain. I suspect that the pattern is due to low sample sizes (the 3 coyotes showing the strong dip have the lowest numbers of barks) and severe non-normality in the distribution of maximum dB frequency data.

*Bark Mean.*--Bark mean frequencies declined slightly due to noise reduction and normalization, and then increased dramatically at the 10-m distance before slowly declining at further distances (Figure 28). Noise reduction evidently removed some of the higher frequency components of the barks, while the playback speaker's overemphasis of high frequencies consequently shifted bark means higher. As the barks traveled to the 500-m and 1,000-m recording sites, attenuation caused a proportional loss

of higher frequencies. The individual differences in values at 1,000-m may be due to measurement error. The method I used for selecting bark segments was based on the time of maximum sound amplitude, which is usually not the midpoint of the sound. As the sound signal got weaker and slightly shorter with distance, background noise could alter the point of maximum amplitude, making proportionally less of the segment encompass the actual bark.

*Bark Standard Deviation.*--The pattern for bark standard deviation (Figure 29) was similar to bark mean frequency. Standard deviations declined with noise reduction, as bark energy was more tightly focused around the mean frequency. Standard deviations shot up at the 10-m distance, when the playback system broadened bark energy by emphasizing higher frequencies. This effect was non-linear, and barks with lower means were more strongly affected. Standard deviation then tended to decrease with increasing distance, as higher frequencies were attenuated. The individuals showing the most fluctuation in values at 500-m and 1,000-m were the coyotes with the lowest initial means.

*Bark Skewness and Kurtosis.*--Skewness was decreased by noise reduction, and then altered significantly by playback (Figure 30). Skewness was changed at the 10-m distance roughly in relation to the mean frequency of the noise-reduced barks; it increased if the mean frequency was above 1200 Hz, and decreased if the mean was below this level. Skewness was highly negatively correlated with mean ( $r < -0.80$ ) at all distances except the 10-m recording ( $r = -0.199$ ), so at most distances lower means meant more skewed sound energy distributions, and the pattern of the data can be explained based on mean frequency values. The playback speaker's emphasis of higher frequencies

apparently disrupted the normal relationship between mean and skewness, but this relationship was restored by attenuation of high frequencies during sound transmission. The pattern for kurtosis (Figure 31) was similar to that for skewness. These 2 measures were indeed highly correlated ( $r > 0.66$  for all distances), so trends in kurtosis were based on the pattern for skewness.

*HNR and HNR Frequency.*--Noise reduction increased HNR values slightly, and then HNR decreased with increasing distance from the playback (Figure 32). This pattern was similar to that seen for bark structure, for the same reasons. The peak in HNR values at 500-m for some individuals may have been due to my method of selecting bark segments for HNR. As with the spectral moments, my program selected a region around the bark's maximum amplitude. But unlike the spectral moment procedure, these barks were not bandpass filtered first, so low frequency noise at 500-m and 1,000-m may have biased segment selection towards regions with less bark energy.

HNR frequency did not vary for the first 3 distances, but then it slightly increased at 500-m and 1,000-m (Figure 33). The increase at greater distances was probably due to the way my program selected segments for analysis. The overall variability in the individual means, particularly for higher HNR frequencies, was probably due to low sample sizes for M-5429 and F-5438 and severe non-normality in the distribution of HNR frequency data.

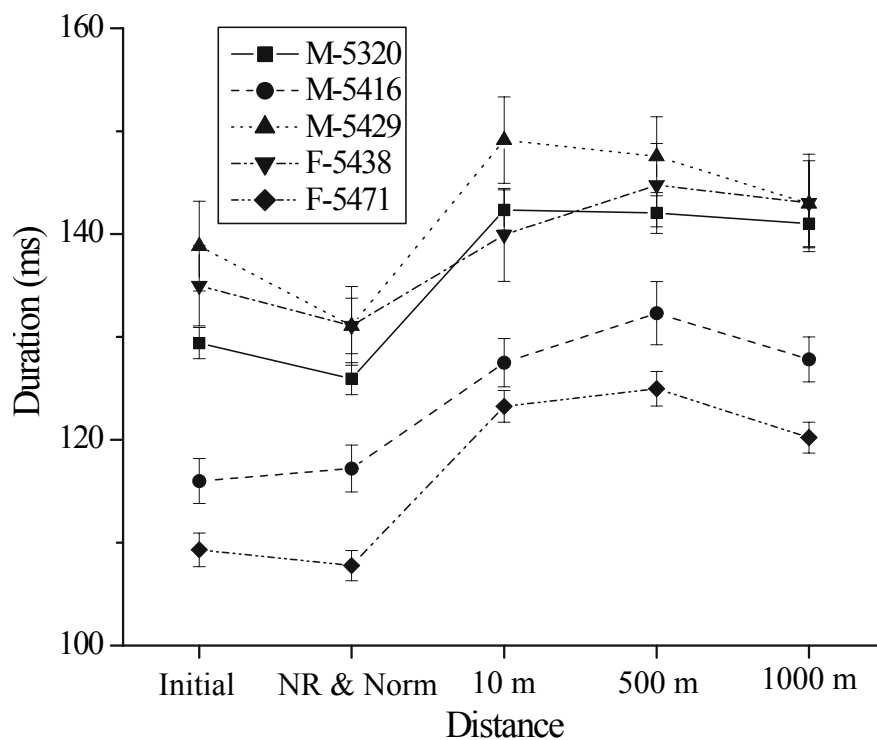


Figure 24. Bark duration: mean and standard error for each individual at each distance.

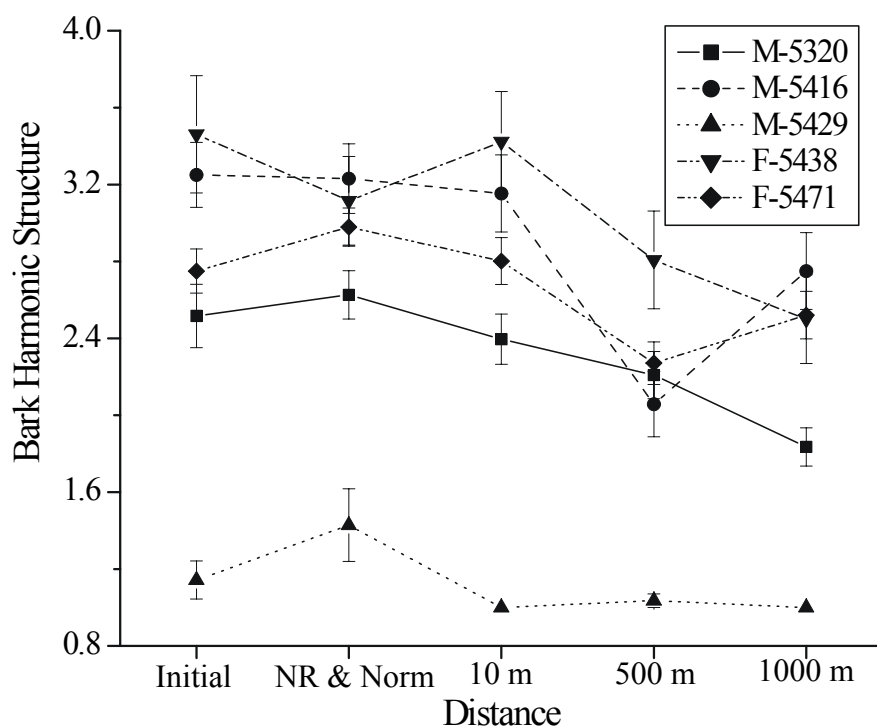


Figure 25. Bark harmonic structure: mean and standard error for each individual at each distance.

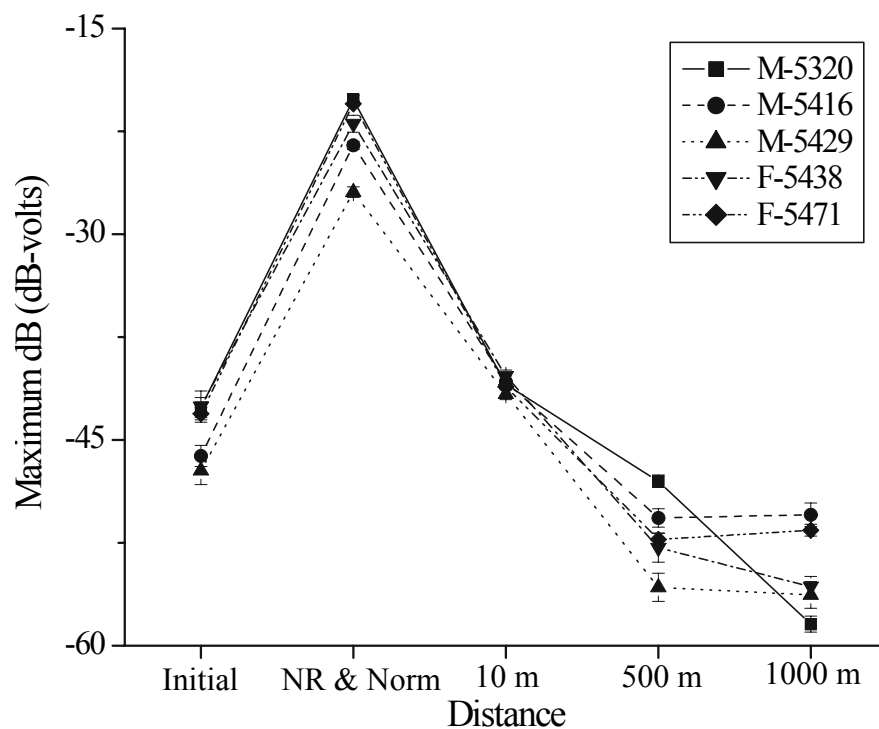


Figure 26. Maximum dB: mean and standard error for each individual at each distance.

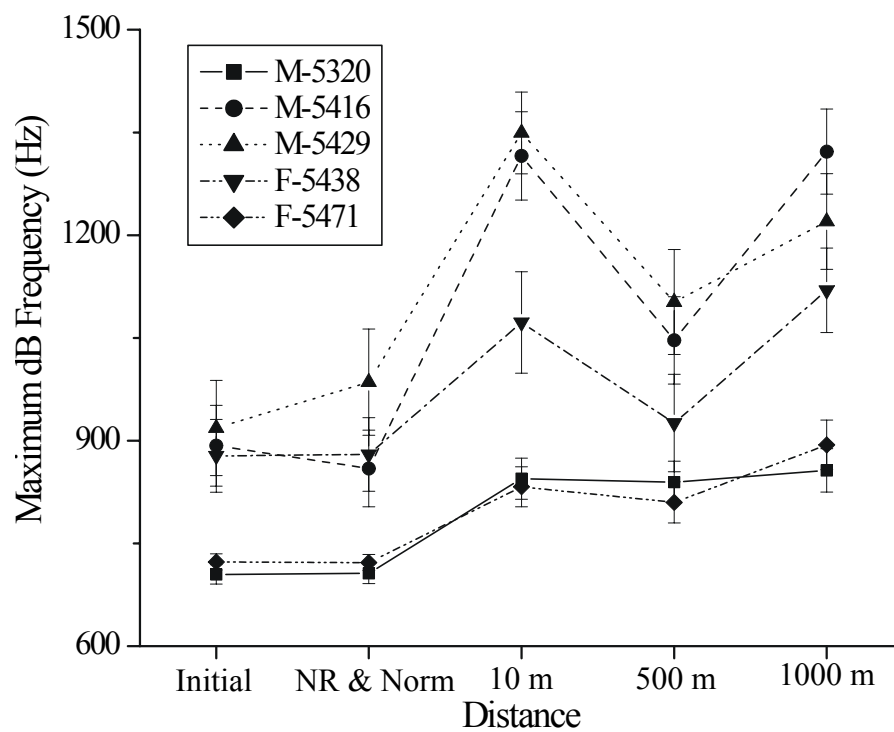


Figure 27. Maximum dB frequency: mean and standard error for each individual at each distance.



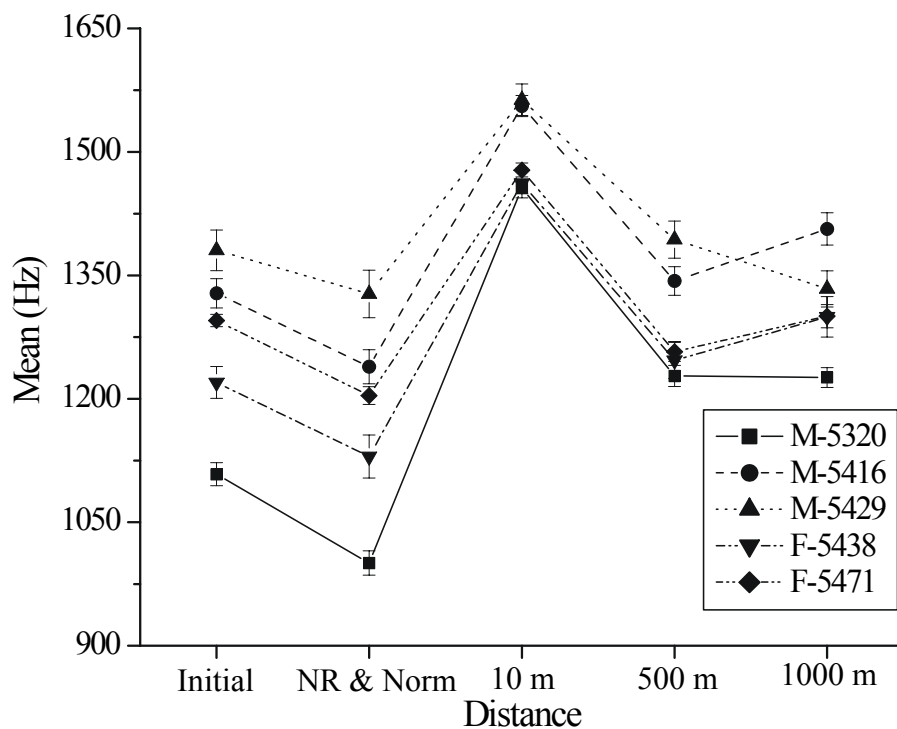


Figure 28. Bark mean: mean and standard error for each individual at each distance.

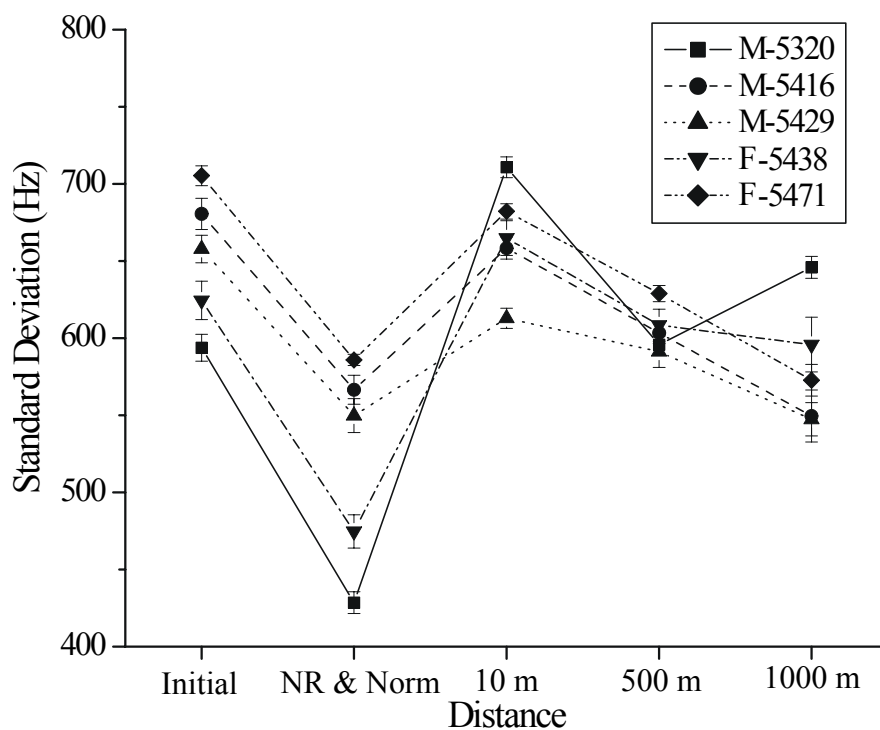


Figure 29. Bark standard deviation: mean and standard error for each individual at each distance.

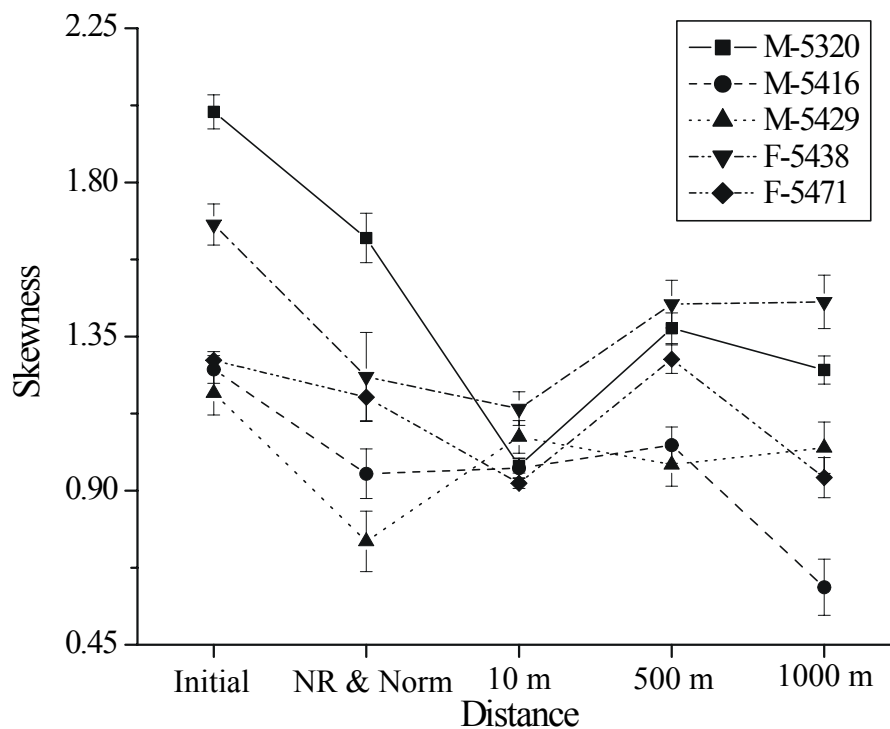


Figure 30. Bark skewness: mean and standard error for each individual at each distance.

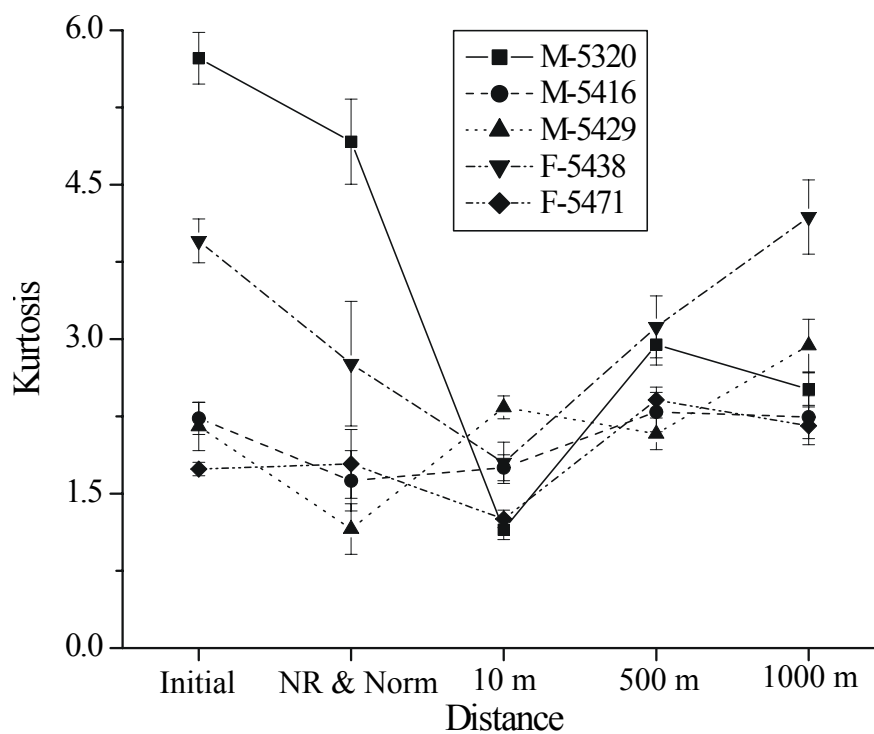


Figure 31. Bark kurtosis: mean and standard error for each individual at each distance.

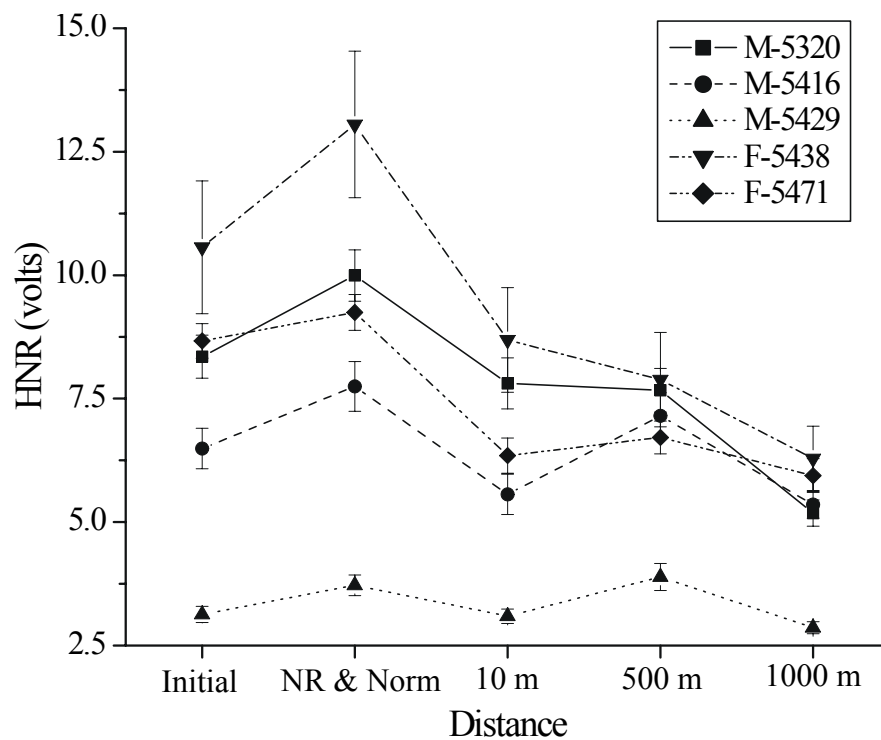


Figure 32. HNR: mean and standard error for each individual at each distance.

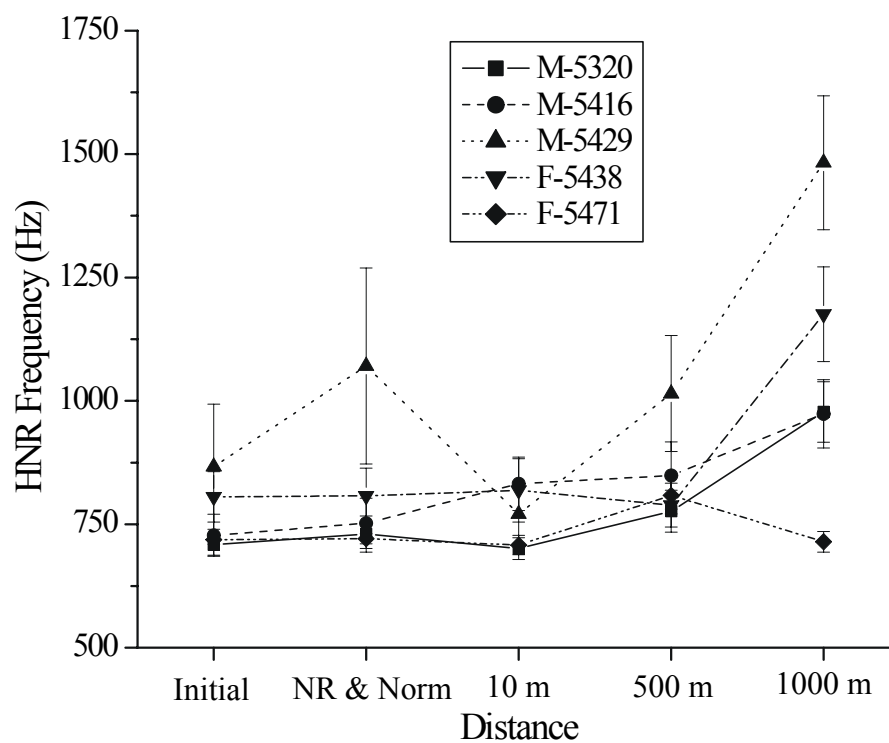


Figure 33. HNR frequency: mean and standard error for each individual at each distance.

#### **APPENDIX 4. METHODS OF LOCATING COLLARED COYOTES**

Radio collared coyotes were located 9 different ways during the study, and each location method had different positional errors, limitations and biases. Coyotes were located by capture, regular telemetry, vocalization trial telemetry, aerial telemetry, visual sightings, vocalization trial sightings, automated receiver, GPS collar, and mortality sites.

Capture locations were always used in the data set of independent locations (except in the single case of a recaptured GPS-collared individual), and were recorded with GPS units accurate to within 10 m. Time of capture could not be determined, and was assumed to be midnight on the morning of capture. Capture locations prior to November 1998 were biased towards roads, and subsequent captures were biased towards fence lines. These biases reflect typical sites for leghold traps and neck snares.

Regular telemetry refers to periodic tracking efforts by 1 or 2 researchers using handheld Yagi antennas; we attempted to locate all collared animals at least once per week. The minimum criteria for a telemetry fix were: (1) 3 bearings; (2) all bearings taken within a 2 hour period (67% of locations were completed in 60 minutes or less); (3) spread of bearing angles greater than 45 degrees (low angles produced locations with high error along the bearing axis); (4) locations placing animals at canyon mouths had to include at least 1 bearing from high ground; (5) error ellipse for the location less than 30 ha for triangulations calculated using LOCATE II (V. Nams, Truro, Nova Scotia, Canada); and (6) bearings used in a fix had to be consistent with bearings that were not used (allowing for bounce, distance to animal, and coyote movements). These criteria were occasionally relaxed if coyotes were in inaccessible locations.

From July 1999 to February 2000, regular telemetry was conducted around the clock, but during all other time periods telemetry efforts were temporally biased to daylight hours. Telemetry accuracy was assessed by locating stationary collars in unknown locations. All researchers located 5 to 10 test collars as part of their initial telemetry training. The average location error was  $209 \text{ m} \pm 183 \text{ m}$  ( $\bar{x} \pm \text{SD}$ ,  $n = 170$ ); median accuracy was 155 m, with 75% within 293 m and 90% within 441 m of the true location (determined by GPS). In addition, there were 6 instances where coyotes wearing active GPS collars were located via regular telemetry. These locations had an average error of 330 m (range 42 m to 636 m).

Vocalization trial telemetry involved 3 to 5 researchers using handheld Yagi antennas to take roughly concurrent bearings on 2 to 6 coyotes during a 3-hr period. The same minimum criteria from regular telemetry also applied to trial telemetry, except that: (1) bearings for each location were all taken within a 30-minute period; and (2) the spread of bearing angles could be as low as 30 degrees. When determining social status, only 1 trial telemetry location was used per animal from a given trial. Locations from the hour following an experimental playback were excluded; otherwise the location was the earliest one with an estimated 95% error below 10 ha, or the best location with an error below 30 ha. During the 2-hr period following a trial, researchers would occasionally shift to 1 or more additional locations to locate coyotes that were not involved in the trial. Locations collected in post-trial efforts were considered part of that trial, but were subject to the minimum criteria for regular telemetry. Vocalization trial telemetry was normally conducted between 0100 and 0900. The accuracy of trial telemetry was assessed using

locations on a coyote with VHF and GPS collars; the mean location error was  $289 \text{ m} \pm 184 \text{ m}$  ( $\bar{x} \pm \text{SD}$ ,  $n = 38$  locations from 6 trials).

Airplane-based aerial telemetry was provided periodically by the California Department of Fish and Game. Aerial telemetry was only conducted on coyotes that could not be regularly located with ground-based telemetry. Flights were between 0730 and 1200, and location error (based on GPS locations of 8 mortalities) was 271 m (range 31 m to 494 m).

Visual sightings included sightings of collared individuals where the identity of the coyote could be confirmed with a telemetry receiver or on the basis of ear tag and collar colors or other identifying features. Sightings included chance observations as well as visuals of coyotes that were actively being radio tracked. Third party sightings were occasionally included if the person who saw the coyote was familiar enough with the research site to give an accurate location. Researchers occasionally walked to the site where the coyote was seen, but more commonly we recorded our position with a GPS and estimated the distance and bearing to the coyote, noting any landmarks near the animal. We then determined the coyote's position using the site GIS, which included 1-m aerial photos and contour lines. Visuals were biased to daylight hours and were more likely near roads and open terrain. Two sightings of a GPS collared individual had location errors of 81 m and 126 m.

Vocalization trial sightings included visual locations during or within approximately 30 minutes of a vocalization trial. During playback trials researchers actively tried to spot coyotes with the help of telemetry bearings and spotting scopes or binoculars. Locations were determined using the site GIS, and when multiple researchers

saw the same individual they plotted their data together and agreed on the best location. Vocalization trial sightings were collected between 0500 and 1000, and were biased towards open terrain and preferred telemetry stations.

Automated receivers (SRX 400, Lotek Wireless, Newmarket, Ontario, Canada) were used regularly, most commonly at audio playback sites. The gain on the receiver was set so that radio collars were not normally detected beyond 100 m from the receiver, and detections were never used unless the power reading exceeded 200 (238 was the maximum reading). This ensured that coyotes had to be well within 100 m of the receiver to be recorded. The detection with the highest power level over an 8-hr period was saved as an automated receiver location. If multiple 8-hr periods had locations for the same coyote while the receiver was at a given location, only the first and last location was retained. Automated receivers were placed in randomly selected locations prior to April 2001; after this date researchers had more control over receiver placement, which resulted in a slight road bias.

Six GPS collars were placed on coyotes; 1 of these was not recovered due to failure of the drop-off mechanism. The collars recorded locations every 15 minutes for approximately 4 weeks. The first hour of GPS data was discarded for each animal, as was the first location whenever 2 locations were recorded within 4 minutes. For the 2 coyotes where VHF telemetry data were also available, the large number of locations from the GPS collars would bias analyses towards the time period when the GPS collar was worn. For these individuals, I randomly selected 1 location every fifth day for use in the data set used to determine social status. This rate of 0.20 locations per day was within the range of location rates for VHF collared coyotes having 30 or more locations.

GPS collar locations had 4 possible accuracy levels (3D+, 3D, 2D, and 1D), depending on the number of satellites being received by the collar. Locations at the 3D+ level were recorded prior to release for 4 individuals, and these were an average of 2 m (range 1 m to 4 m) from locations obtained with a handheld GPS receiver. These locations were therefore within the 10-m accuracy that could be expected with GPS. The distance error of 1D and 2D locations was assessed by looking at times when 1D and 2D locations were between higher accuracy 3D or 3D+ points. The high accuracy positions had to be within 25 m and 1 hr of each other. The 1D and 2D positions were an average of  $60 \text{ m} \pm 87 \text{ m}$  ( $\bar{x} \pm \text{SD}$ ,  $n = 13$ , range 4 m to 335 m) away from the prior and subsequent 3D or 3D+ locations. When the 1 anomalously high error was removed (under the assumption that the coyote may have made a brief foray and returned to her original position), the average error was  $37 \text{ m} \pm 29 \text{ m}$  ( $\bar{x} \pm \text{SD}$ ,  $n = 12$ , range 4 m to 80 m). Location error for GPS collar positions therefore ranges from about 10 m to 100 m, depending on the accuracy rating.

Mortality locations were used whenever they could be determined via ground-based triangulation, aerial telemetry, or walking in on a mortality site. Accuracy of mortality locations depended on the location method. In some cases collars were clearly moved by shooters and poachers, and these locations were not used. I estimated the date of death based on the condition of the remains and the most recent locations; in many cases the date could be determined within a few days.



## **APPENDIX 5. MODEL SET CONSTRUCTION FOR PLAYBACK RESPONSE ANALYSES**

### **Vocal Response Confirmatory Analysis**

*Initial predictions.*--For the initial model set, each variable and interaction was assigned a relative importance ranging from 1 to 5, with lower numbers indicating variables that were predicted to have the greatest influence on coyote vocal responses to playbacks (Table 38). The initial rankings were derived from published research and personal observations.

Social status, playback type, and playback season were all given an importance of 1 because of strong support for their importance in the published literature. Gese and Ruff (1998) found strong social status effects on coyote spontaneous howls, with transients never howling and alphas howling the most. They also noted that spontaneous howls were most likely during the breeding and recovery seasons. Okoniewski and Chambers (1984) noted a similar seasonal effect with elicited playback responses, as well as a trend towards more responses to human imitations of howling than to a siren.

Wind was also expected to be important, because high wind speeds would make it more difficult for coyotes to hear playbacks and for researchers to hear coyote responses. Wolfe (1974) reported that high wind decreased responses to his siren.

Playback time and the presence of vocalizations within 5 minutes of playback were predicted to be of intermediate utility. Gaines et al. (1995) found that playback responses were more likely at dawn and dusk, and other studies have found peaks in spontaneous vocalizations at dawn and dusk (Laundré 1981, Walsh and Inglis 1989). However, I was not sure how pronounced the dawn peak would be over the 5-hour period

(relative to sunrise) during which playbacks occurred in this experiment. Vocalizations before playback were expected to reduce coyote responsiveness to playbacks (based on personal observations during pilot studies), but I expected this effect to be masked by the difficulty of determining whether coyotes were responding to playback or continuing their vocalization bout.

I expected playback location and lunar phase to be less important. Fulmer (1990) documented more vocal responses to playbacks within a coyote's territory, but I predicted that location of playback would not have a big effect on vocal responses. Canid vocalizations are generally thought to be a declaration of territoriality as well as a spacing mechanism for avoiding direct confrontation (Harrington and Mech 1979, Fulmer 1990, Jaeger et al. 1996). If this is the case, then coyotes should respond approximately equally to playbacks inside or outside of their territory because they are warning intruders to leave in the former case and advertising territorial occupancy in the latter situation. Lunar phase has been shown to have an effect on coyote vocalizations in at least 1 study (Bender et al. 1996), but other studies have found no effect (Walsh and Inglis 1989). I predicted that there would be more vocal responses when the moon was up and bright because coyotes would be more active with the improved lighting.

Sex and the interaction of status and playback type were not expected to be particularly important. Gese and Ruff (1998) found no effect of sex on spontaneous vocalization rates, but I predicted that males would howl more because they tend to be more aggressive. I expected to find an interaction between social status and playback type because I thought it would be likely that transients would show a low overall response rate while alphas and betas would vary their response rates depending on the

type of playback. I also expected that betas might respond to playbacks differently from alphas; for example their lack of experience might lead them to vocalize more in response to an obviously artificial playback (e.g. the siren) than alphas.

*Data set diagnostics.*--I used univariate contingency table analysis to look for zero cells and to verify my predictions of variable importance. Playback type and wind speed both had zero cells; coyotes never responded vocally to control playbacks or in high wind (greater than 5 km per hour). These results showed that coyotes were responding to playback and not some artifact of the experimental design, plus they documented the importance of wind for obtaining vocal responses to playback. Records with high wind or control playbacks were then deleted from the data set to avoid biasing the analysis, and wind speed was excluded from the analysis (all records had low wind speed). The status by playback type interaction also had zero cells, because there was only 1 vocal response by a transient. I solved this problem by grouping all the transient data while maintaining the interaction for alphas and betas (Hosmer and Lemeshow 2000: 136-137). This method had the disadvantage of producing non-nested models (compared to models without the modified interaction) that could not be used together for model parameter averaging.

The contingency table analysis showed that season was probably much less important than I had predicted and that sex and the status by playback type interaction were much more important (although the interaction effect could not be evaluated separately from the effects of status and playback type). The importance of these variables was adjusted accordingly (Table 38).

*Model set.*--The initial model set was constructed based on variable importance. There were 2 subsets; one contained the status by playback type interaction and the other did not. Within each subset, the global model contained all variables. Reduced models were enumerated according to the rule that a variable could only be removed if all variables with lesser importance were also removed. This resulted in a total set of 18 models (Table 39). Because the variable “Status by Type” was not a complete interaction, models with “Status” and “Type” were not nested within the set of models containing “Status by Type”. Consequently models from each subset could not be combined in the final model set used for parameter averaging. Models with “Status by Type” always had lower Akaike weights ( $\omega_i$ ) and higher small sample Akaike’s Information Criterion ( $AIC_c$ ) values than comparable models with social status and playback type. The summed Akaike weights for these models was only 0.11 (out of 1.0 for the entire model set), indicating a low weight of evidence in favor of using the interaction of status and playback type. The final model set therefore included only the 8 models without “Status by Type” that also had Akaike weights greater than 0.01 (Table 26).

### **Vocal Response Exploratory Analysis**

*Model set development.*--The initial confirmatory model set was refit after removing records with missing barometric pressure data and records for transients (because their presence produced zero cells in interaction terms). With the aim of minimizing  $AIC_c$ , I constructed a series of models by removing or adding one variable at a time and fitting the new model. I began with Model 4, which had the lowest  $AIC_c$ . Season, vocalizations before playback, and the status by playback type interaction all increased  $AIC_c$ , while social status, sex, playback type, playback location, and moon were all important

(decreased  $AIC_c$ ). Barometric pressure was not important, but net barometric pressure change had an effect. Playback time was only useful when the categories were collapsed into pre-dawn (between 3 hours and 1 hour before sunrise) and later (sunrise and 1 hour after sunrise) playbacks.

I examined all 2-way interactions between social status, sex, playback type, playback time, moon, and net barometric change. Social status by sex, social status by time, sex by time, and sex by net barometric change all reduced  $AIC_c$  or increased it less than 1 unit.

The final model set contained the model with the lowest  $AIC_c$  and all models within 2  $AIC_c$  units (Table 28). Because interaction terms dramatically increased model complexity, models that added an interaction term had to be within 1  $AIC_c$  unit of the best model.

### **Movement Response Confirmatory Analysis**

*Initial predictions.*--As with the vocal response analysis, each variable and interaction was assigned a relative importance ranging from 1 to 5 (Table 40). Predictions were based on the assumption that coyotes would treat at least a few of the playback types as territorial intrusions by competitors.

Social status, season, and playback type were given an importance of 1. Social status is known to affect numerous aspects of coyote behavior (Camenzind 1978, Andelt 1985, Bekoff and Wells 1986), plus Gese (2001) found that alphas were more active in territorial defense than betas. He also noted a peak in territorial behavior extending from the breeding season to soon after pups emerged from the den. Playback type was expected to be important because coyotes should treat some playbacks as competitors

(e.g. group howls), some as potential food (e.g. human imitations of prey), and others as curious events to investigate (e.g. siren, assuming that this sound was not mistaken for a competitor). Since territorial defense and food acquisition were presumably more important than investigating odd events, I expected to see different approach rates for different playback types.

Playback location and the interaction of social status and playback type were predicted to be slightly less important. I expected that coyotes would be more likely to approach playbacks within their home range because their familiarity with the area would make them more comfortable investigating the site. In addition, Gese (2001) found that coyotes would readily approach and challenge intruders but would stop chasing them at the territory boundary. I expected a strong interaction between playback type and social status, but I also felt that the relationship would be difficult to detect given the sample size and number of model terms (the interaction required 8 parameters). Alphas and betas were expected to respond to coyote vocalizations much more strongly than transients, and all coyotes were expected to respond approximately equally to non-coyote playbacks.

Coyote sex and the presence of a vocal response were given an intermediate level of importance. Wagner (1997: 55) noted that males were more likely than females to be killed with calling and shooting, and Gese (2001) found that males were more involved in territorial defense. I predicted that vocal responses would increase the chance of an approach response as coyotes investigated whether their response convinced the (presumed) intruder to leave the area.

Vocalizations before playback, playback time, and the interaction of social status and playback location were given an initial importance of 4. Vocalizations within 5 minutes of playback were predicted to decrease the chance of an approach because coyotes would have to split their attention between multiple stimuli. Playback time was expected to be important because of the documented peak in activity near sunrise (Andelt and Gipson 1979, Andelt 1985). I expected to find an interaction between social status and playback location because I predicted that transients would not attempt to defend their home range, while territorial animals would respond more aggressively to playbacks within their home range.

The lowest importance rating was given to wind speed and lunar phase. High winds were predicted to impede coyotes' ability to hear playbacks. Lunar phase was not expected to be important, but was included because Bender et al. (1996) predicted higher rates of activity when the moon was up and bright.

*Data set diagnostics.*--Contingency table analysis found no zero cells in the movement response data. The analysis did, however, result in changed importance for several variables when the results showed that my initial predictions were poor (Table 40).

*Model set.*--The initial model set was constructed as described above for the vocal response confirmatory model set. This procedure resulted in a total set of 34 models (Table 41). The final model set included only the 15 models with Akaike weights ( $\omega_i$ ) greater than 0.01; this criteria excluded all 17 models that contained the interaction term between social status and playback type.

### **Movement Response Exploratory Analysis**

The initial movement response confirmatory model set was refit after records with missing barometric pressure data were removed from the data set. I then fit a series of models according to the procedure described for the vocal response exploratory analysis. Social status, playback type, playback location, vocalizations before playback, and season were all important variables. Season was even more important when the 4 categories were combined into Breeding and Whelping (1 January to 15 June) and Rearing and Recovery (16 June to 31 December). Playback time was only important when it was divided into 2 categories: after sunrise and earlier. Wind, moon, sex, and net barometric trend each increased  $AIC_c$  less than 2 units. I examined the effect of including 2-way interactions between social status, playback type, playback time, playback location, vocalizations before playback, and season. All of the interactions increased  $AIC_c$  by more than 1 unit and were excluded. The final model set contained 11 models (Table 32).



Table 38. Importance of variables used in the confirmatory vocal response analysis.

Variable	Initial Importance	$\chi^2$ <sup>1</sup>	df	p <sup>1</sup>	Final Importance
Social Status	1	23.8	2	< 0.001	1
Playback Type <sup>2</sup>	1	34.0	3	< 0.001	1
Season	1	0.7	3	0.862	5
Wind <sup>2</sup>	2	N/A	1	N/A	N/A
Playback Time	3	5.0	4	0.288	3
Vocals Before PB	3	2.0	1	0.161	3
Playback Location	4	0.2	1	0.644	4
Lunar Phase	4	2.0	1	0.162	4
Sex	5	11.6	1	< 0.001	1
Status by Type <sup>3</sup>	5	58.8	8	< 0.001	1

<sup>1</sup> Contingency table analysis results were based on the final data set, with 575 records.

<sup>2</sup> High wind and control playback records were excluded from the data set because of zero cells.

<sup>3</sup> Status by Type replaces Social Status and Playback Type in the appropriate models. This variable models the interaction effect of status and playback type, but groups all transient data.

Table 39. Initial model set for confirmatory vocal response analysis. Notation follows Burnham and Anderson (2002).

Model <sup>1</sup>	K	AIC <sub>c</sub>	$\Delta_i$	$\omega_i$
1: Stat + Typ + Sex + Time + VB4 + Loc + Moon + Seas	17	302.6	9.8	0.003
2: Stat + Typ + Sex + Time + VB4 + Loc + Moon	14	297.9	5.0	0.032
3: Stat + Typ + Sex + Time + VB4 + Loc	13	298.4	5.5	0.025
4: Stat + Typ + Sex + Time + VB4 + Moon	13	296.5	3.7	0.063
5: Stat + Typ + Sex + Time + VB4	12	296.8	4.0	0.053
6: Stat + Typ + Sex + Time	11	296.3	3.4	0.071
7: Stat + Typ + Sex + VB4	8	293.8	1.0	0.239
8: Stat + Typ + Sex	7	292.8	0.0	0.393
9: Stat + Typ	6	299.5	6.6	0.014
10: ST + Sex + Time + VB4 + Loc + Moon + Seas	20	306.8	14.0	0.000
11: ST + Sex + Time + VB4 + Loc + Moon	17	301.6	8.8	0.005
12: ST + Sex + Time + VB4 + Loc	16	302.1	9.2	0.004
13: ST + Sex + Time + VB4 + Moon	16	300.3	7.4	0.010
14: ST + Sex + Time + VB4	15	300.6	7.7	0.008
15: ST + Sex + Time	14	300.1	7.3	0.011
16: ST + Sex + VB4	11	298.3	5.5	0.025
17: ST + Sex	10	297.2	4.4	0.044
18: ST	9	304.0	11.1	0.002

<sup>1</sup> Stat = Status, Typ = PB Type, ST = Status by Type, VB4 = Vocals before PB, Loc = PB Location, Seas = Season.

Table 40. Importance of variables used in the confirmatory movement response analysis.

Variable	Initial Importance	$\chi^2$ <sup>1</sup>	df	p <sup>1</sup>	Final Importance
Social Status	1	8.0	2	0.019	1
Playback Type	1	12.0	4	0.018	1
Season	1	6.4	3	0.094	1
Playback Location	2	3.5	1	0.060	2
Status*Type <sup>2</sup>	2	23.1	14	0.059	1
Vocal Response	3	1.6	1	0.205	3
Sex	3	0.6	1	0.437	4
Vocals Before PB	4	3.9	1	0.049	2
Playback Time	4	4.3	4	0.361	4
Status*Location <sup>2</sup>	4	14.6	5	0.012	2
Wind	5	2.3	1	0.128	3
Lunar Phase	5	1.7	1	0.187	3

<sup>1</sup> Contingency table analysis results were based on the final data set, with 448 records.

<sup>2</sup> Interactions were examined based on contingency tables containing each possible combination of the 2 variables. The results therefore represent the combined effect of the variables and their interaction.

Table 41. Initial model set for confirmatory movement response analysis.

Model <sup>1</sup>	K	AIC <sub>c</sub>	$\Delta_i$	$\omega_i$
1: Stat + Typ + S*T + Seas + Loc + S*L + VB4 + Voc + Wnd + Moon + Sex + Time	30	490.3	23.7	0.000
2: Stat + Typ + S*T + Seas + Loc + S*L + VB4 + Voc + Wnd + Moon + Sex	26	483.9	17.3	0.000
3: Stat + Typ + S*T + Seas + Loc + S*L + VB4 + Voc + Wnd + Moon + Time	29	488.0	21.5	0.000
4: Stat + Typ + S*T + Seas + Loc + S*L + VB4 + Voc + Wnd + Moon	25	481.7	15.1	0.000
5: Stat + Typ + S*T + Seas + Loc + S*L + VB4 + Voc + Wnd	24	482.8	16.2	0.000
6: Stat + Typ + S*T + Seas + Loc + S*L + VB4 + Voc + Moon	24	482.9	16.4	0.000
7: Stat + Typ + S*T + Seas + Loc + S*L + VB4 + Wnd + Moon	24	479.5	12.9	0.000
8: Stat + Typ + S*T + Seas + Loc + S*L + VB4 + Voc	23	483.2	16.6	0.000
9: Stat + Typ + S*T + Seas + Loc + S*L + VB4 + Wnd	23	480.7	14.1	0.000
10: Stat + Typ + S*T + Seas + Loc + S*L + VB4 + Moon	23	480.8	14.3	0.000
11: Stat + Typ + S*T + Seas + Loc + S*L + VB4	22	481.2	14.6	0.000
12: Stat + Typ + S*T + Seas + Loc + S*L	21	481.5	14.9	0.000
13: Stat + Typ + S*T + Seas + Loc + VB4	20	480.4	13.8	0.000
14: Stat + Typ + S*T + Seas + VB4	19	482.8	16.3	0.000
15: Stat + Typ + S*T + Seas + Loc	19	480.7	14.1	0.000
16: Stat + Typ + S*T + Seas	18	483.2	16.6	0.000
17: Stat + Typ + S*T	15	483.8	17.2	0.000
18: Stat + Typ + Seas + Loc + S*L + VB4 + Voc + Wnd + Moon + Sex + Time	22	476.6	10.0	0.001
19: Stat + Typ + Seas + Loc + S*L + VB4 + Voc + Wnd + Moon + Sex	18	470.8	4.2	0.020
20: Stat + Typ + Seas + Loc + S*L + VB4 + Voc + Wnd + Moon + Time	21	474.5	7.9	0.003
21: Stat + Typ + Seas + Loc + S*L + VB4 + Voc + Wnd + Moon	17	468.7	2.1	0.057
22: Stat + Typ + Seas + Loc + S*L + VB4 + Voc + Wnd	16	469.7	3.1	0.035
23: Stat + Typ + Seas + Loc + S*L + VB4 + Voc + Moon	16	470.0	3.5	0.029
24: Stat + Typ + Seas + Loc + S*L + VB4 + Wnd + Moon	16	466.6	0.0	0.163
25: Stat + Typ + Seas + Loc + S*L + VB4 + Voc	15	470.2	3.6	0.027
26: Stat + Typ + Seas + Loc + S*L + VB4 + Wnd	15	467.6	1.1	0.096
27: Stat + Typ + Seas + Loc + S*L + VB4 + Moon	15	468.0	1.5	0.079
28: Stat + Typ + Seas + Loc + S*L + VB4	14	468.3	1.7	0.070
29: Stat + Typ + Seas + Loc + S*L	13	468.6	2.1	0.058
30: Stat + Typ + Seas + Loc + VB4	12	466.9	0.3	0.140
31: Stat + Typ + Seas + VB4	11	469.0	2.5	0.048
32: Stat + Typ + Seas + Loc	11	467.3	0.8	0.112
33: Stat + Typ + Seas	10	469.6	3.0	0.037
34: Stat + Typ	7	470.3	3.8	0.025

<sup>1</sup> Stat = Status, Typ = PB Type, S\*T = Status\*Type interaction, Seas = Season, Loc = PB Location, S\*L =

Status\*Location interaction, VB4 = Vocals before PB, Voc = Vocal Response, Wnd = Wind.

### LITERATURE CITED

- Alcorn, J. R. 1946. On the decoying of coyotes. *Journal of Mammalogy* 27:122-126.
- Andelt, W. F. 1985. Behavioral ecology of coyotes in south Texas. *Wildlife Monographs* 94:1-45.
- Andelt, W. F., and P. S. Gipson. 1979. Home Range, Activity, and Daily Movements of Coyotes. *Journal of Wildlife Management* 43:944-951.
- Andelt, W. F., R. L. Phillips, K. S. Gruver, and J. W. Guthrie. 1999. Coyote predation on domestic sheep deterred with electronic dog-training collar. *Wildlife Society Bulletin* 27:12-18.
- Bachorowski, J. A., and M. J. Owren. 1999. Acoustic correlates of talker sex and individual talker identity are present in a short vowel segment produced in running speech. *Journal of the Acoustical Society of America* 106:1054-1063.
- Ballintijn, M. R., and C. Ten Cate. 1997. Sex differences in the vocalizations and syrinx of the Collared Dove (*Streptopelia decaocto*). *Auk* 114:22-39.
- Beaudette, T. 1996. Calling coyotes. *Wildlife Control Technology*. Sep: 46-49.
- Bekoff, M., and M. C. Wells. 1986. Social ecology and behavior of coyotes. *Advances in the Study of Behavior* 16:251-338.
- Bender, D. J., E. M. Bayne, and R. M. Brigham. 1996. Lunar condition influences coyote (*Canis latrans*) howling. *American Midland Naturalist* 136:413-417.
- Black, H. L., and J. S. Green. 1984. Navajo use of mixed-breed dogs for management of predators. *Journal of Range Management* 38:11-15.

- Blejwas, K. M., B. N. Sacks, M. M. Jaeger, and D. R. McCullough. 2002. The effectiveness of selective removal of breeding coyotes in reducing sheep predation. *Journal of Wildlife Management* 66:451-462.
- Bodenchuk, M. J., J. R. Mason, and W. C. Pitt. Economics of predation management in relation to agriculture, wildlife, and human health and safety. In: L. Clark, editor. *Human Conflict with Wildlife: Economic Considerations*. Proceedings of the Third NWRC Special Symposium; 2000 1-3 August 2000; Fort Collins, Colorado, USA. National Wildlife Research Center. p 80-90.
- Breck, S. W., R. Williamson, C. Niemeyer, and J. A. Shivik. 2002. Non-lethal radio activated guard for deterring wolf predation in Idaho: Summary and call for research. *Proceedings of the Vertebrate Pest Conference* 20:223-226.
- Bromley, C., and E. M. Gese. 2001a. Effects of sterilization on territory fidelity and maintenance, pair bonds, and survival rates of free-ranging coyotes. *Canadian Journal of Zoology* 79:386-392.
- , 2001b. Surgical sterilization as a method of reducing coyote predation on domestic sheep. *Journal of Wildlife Management* 65:510-519.
- Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference*. Second edition. Springer, New York, New York, USA.
- Burns, R. J., and G. E. Connolly. 1995. Assessment of potential toxicity of Compound 1080 from livestock protection collars to canines and scavenging birds. *International Biodeterioration & Biodegradation* 36:161-167.

- Burns, R. J., G. E. Connolly, and I. Okuno. 1986. Secondary toxicity of coyotes killed by 1080 single-dose baits. *Proceedings of the Vertebrate Pest Conference* 12:324-329.
- Burns, R. J., H. P. Tietjen, and G. E. Connolly. 1991. Secondary hazard of livestock protection collars to skunks and eagles. *Journal of Wildlife Management* 55:701-704.
- Burns, R. J., D. E. Zemlicka, and P. J. Savarie. 1996. Effectiveness of large livestock protection collars against depredating coyotes. *Wildlife Society Bulletin* 24:123-127.
- California Fish and Game Code. 1998. Trapping practices. Bans use of specified traps and animal poisons. Initiative statute. Sections 3003.1-3003.2, 12005.5.
- Camenzind, F. J. 1978. Behavioral ecology of coyotes on the National Elk Refuge, Jackson, Wyoming. Pages 267-294 *in* M. Bekoff, editor. *Coyotes: Biology, Behavior, and Management*. Academic Press, New York, USA.
- Charrier, I., N. Mathevon, and P. Jouventin. 2002. How does a fur seal mother recognize the voice of her pup? An experimental study of *Arctocephalus tropicalis*. *Journal of Experimental Biology* 205:603-612.
- Cheney, D. L., and R. M. Seyfarth. 1980. Vocal recognition in free-ranging vervet monkeys. *Animal Behaviour* 28:362-367.
- Conner, M. M., M. M. Jaeger, T. J. Weller, and D. R. McCullough. 1998. Effect of coyote removal on sheep depredation in northern California. *Journal of Wildlife Management* 62:690-699.

- Connolly, G. E., R. M. Timm, W. E. Howard, and W. M. Longhurst. 1976. Sheep killing behavior of captive coyotes. *Journal of Wildlife Management* 40:400-407.
- Conover, M. 2002. Resolving human-wildlife conflicts: The science of wildlife damage management. Lewis, New York, New York, USA.
- Conover, M. B., and K. K. Kessler. 1994. Diminished producer participation in an aversive conditioning program to reduce coyote predation on sheep. *Wildlife Society Bulletin* 22:229-233.
- Coolahan, C. 1990. The use of dogs and calls to take coyotes around dens and resting areas. *Proceedings of the Vertebrate Pest Conference* 14:260-262.
- Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400:563-566.
- Dallmann, R., and T. Geissmann. 2001. Different levels of variability in the female song of wild silvery gibbons (*Hylobates moloch*). *Behaviour* 138:629-648.
- Darden, S. K., T. Dabelsteen, and S. B. Pedersen. 2003. A potential tool for swift fox (*Vulpes velox*) conservation: Individuality of long-range barking sequences. *Journal of Mammalogy* 84:1417-1427.
- Davenport, J. W., J. E. Bowns, and J. P. Workman. 1973. Assessment of sheep losses to coyotes. Agricultural Experiment Station Research Report Number 7. Utah State University, Logan, Utah, USA.
- deCalesta, D. S., and M. G. Cropsey. 1978. Field test of a coyote-proof fence. *Wildlife Society Bulletin* 6:256-259.
- Dorrance, M. J., and L. D. Roy. 1976. Predation losses of domestic sheep in Alberta. *Journal of Range Management* 29:457-460.

- Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. *The Birder's Handbook*. Simon and Schuster, New York, New York, USA.
- Emerson, S. B. 2001. Male advertisement calls: Behavioral variation and physical processes. Pages 36-44 *in* M. R. Ryan, editor. *Anuran Communication*. Smithsonian Institution Press, Washington, D.C., USA.
- Fitch, W. T., J. Neubauer, and H. Herzl. 2002. Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production. *Animal Behaviour* 63:407-418.
- Forrest, K., G. Weismer, P. Milenkovic, and R. N. Dougall. 1988. Statistical-analysis of word-initial voiceless obstruents - preliminary data. *Journal of the Acoustical Society of America* 84:115-123.
- Frommolt, K.-H., M. E. Goltsman, and D. W. Macdonald. 2003. Barking foxes, *Alopex lagopus*: field experiments in individual recognition in a territorial mammal. *Animal Behaviour* 65:509-518.
- Fulmer, K. F. 1990. Characterizing the functions of coyote vocalizations through the use of playback. Thesis, University of Idaho, Moscow, Idaho, USA.
- Gaines, W. L., G. K. Neale, and R. H. Naney. 1995. Response of coyotes and gray wolves to simulated howling in north-central Washington. *Northwest Science* 69:217-222.
- Gese, E. M. 2001. Territorial defense by coyotes (*Canis latrans*) in Yellowstone National Park, Wyoming: Who, how, where, when, and why. *Canadian Journal of Zoology* 79:980-987.



- Gese, E. M., and S. Grothe. 1995. Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. *American Midland Naturalist* 133:36-43.
- Gese, E. M., and R. L. Ruff. 1998. Howling by coyotes (*Canis latrans*): Variation among social classes, seasons, and pack size. *Canadian Journal of Zoology* 76:1037-1043.
- Gier, H. T. 1968. Coyotes in Kansas. Kansas State College Agricultural Experiment Station Bulletin 393, Manhattan, Kansas, USA.
- Gouzoules, H., and S. Gouzoules. 2000. Agonistic screams differ among four species of macaques: the significance of motivation-structural rules. *Animal Behaviour* 59:501-512.
- Green, J. S., R. A. Woodruff, and T. T. Tueller. 1984. Livestock-guarding dogs for predator control - costs, benefits, and practicality. *Wildlife Society Bulletin* 12:44-50.
- Grinder, M. I., and P. R. Krausman. 2001. Home range, habitat use, and nocturnal activity of coyotes in an urban environment. *Journal of Wildlife Management* 65:887-898.
- Harrington, F. H., and L. D. Mech. 1979. Wolf howling and its role in territory maintenance. *Behaviour* 68:207-249.
- , 1983. Wolf Pack Spacing: howling as a territory-independent spacing mechanism in a territorial population. *Behavioral Ecology and Sociobiology* 12:161-168.

- Hartwig, S. 2003. Individual identification by acoustic signals as a non-invasive tool in conservation: an approach in the conservation of the African wild dog *Lycaon pictus*. Unpublished manuscript.
- Henke, S. E., and F. C. Bryant. 1999. Effects of coyote removal on the faunal community in western Texas. *Journal of Wildlife Management* 63:1066-1081.
- Holekamp, K. E., E. E. Boydston, M. Szykman, I. Graham, K. J. Nutt, S. Birch, A. Piskiel, and M. Singh. 1999. Vocal recognition in the spotted hyaena and its possible implications regarding the evolution of intelligence. *Animal Behaviour* 58:383-395.
- Hosmer, D. W., and S. Lemeshow. 2000. *Applied Logistic Regression*. Wiley Series in Probability and Statistics. Second Edition edition. John Wiley and Sons, New York, New York, USA.
- Jaeger, M. M., R. K. Pandit, and E. Haque. 1996. Seasonal differences in territorial behavior by golden jackals in Bangladesh: howling versus confrontation. *Journal of Mammalogy* 77:768-775.
- Jouventin, P., T. Aubin, and T. Lengagne. 1999. Finding a parent in a king penguin colony: the acoustic system of individual recognition. *Animal Behaviour* 57:1175-1183.
- Kazial, K. A., S. C. Burnett, and W. M. Masters. 2001. Individual and group variation in echolocation calls of big brown bats, *Eptesicus fuscus* (Chiroptera : Vespertilionidae). *Journal of Mammalogy* 82:339-351.

- Kitchen, A. M., E. M. Gese, and E. R. Schauster. 2000. Changes in coyote activity patterns due to reduced exposure to human persecution. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 78:853-857.
- Klecka, W. R. 1980. Discriminant Analysis. Sage University Papers series on Quantitative Applications in the Social Sciences, 07-019. Sage, Newbury Park, California, USA.
- Knowlton, F. F., E. M. Gese, and M. M. Jaeger. 1999. Coyote depredation control: An interface between biology and management. *Journal of Range Management* 52:398-412.
- Koehler, A. E., R. E. Marsh, and T. P. Salmon. 1990. Frightening methods and devices/stimuli to prevent animal damage - a review. *Proceedings of the Vertebrate Pest Conference* 14:168-173.
- Lambrechts, M. M., and A. A. Dhondt. 1995. Individual voice discrimination in birds. Pages 115-139 in D. M. Power, editor. *Current Ornithology*. Volume 12. Plenum, New York, New York, USA.
- Laundré, J. W. 1981. Temporal variation in coyote vocalization rates. *Journal of Wildlife Management* 45:767-769.
- Lehner, P. N. 1978. Coyote vocalizations: a lexicon and comparisons with other canids. *Animal Behaviour* 26:712-722.
- Lehner, P. N., R. Krumm, and A. T. Cringan. 1976. Tests for olfactory repellents for coyotes and dogs. *Journal of Wildlife Management* 40:145-150.
- Linhart, S. B., G. J. Dasch, R. R. Johnson, J. D. Roberts, and C. J. Packham. 1992. Electronic frightening devices for reducing coyote depredation on domestic

- sheep: Efficacy under range conditions and operational use. *Proceedings of the Vertebrate Pest Conference* 15:386-392.
- Linhart, S. B., R. T. Sterner, G. J. Dasch, and J. W. Theade. 1984. Efficacy of light and sound stimuli for reducing coyote predation upon pastured sheep. *Protection Ecology* 6:75-84.
- Mason, J. R., W. C. Pitt, and M. J. Bodenchuk. 2002. Factors influencing the efficiency of fixed wing aerial hunting for coyotes in the western United States. *International Biodeterioration & Biodegradation* 49:189-197.
- McCarley, H. 1975. Long-distance vocalizations of coyotes (*Canis latrans*). *Journal of Mammalogy* 56:847-856.
- McComb, K., C. Moss, S. Sayialel, and L. Baker. 2000. Unusually extensive networks of vocal recognition in African elephants. *Animal Behaviour* 59:1103-1109.
- McComb, K., D. Reby, L. Baker, C. Moss, and S. Sayialel. 2003. Long-distance communication of acoustic cues to social identity in African elephants. *Animal Behaviour* 65:317-329.
- McCowan, B., and S. L. Hooper. 2002. Individual acoustic variation in Belding's ground squirrel alarm chirps in the High Sierra Nevada. *Journal of the Acoustical Society of America* 111:1157-1160.
- McCowan, B., and D. Reiss. 2001. The fallacy of 'signature whistles' in bottlenose dolphins: a comparative perspective of 'signature information' in animal vocalizations. *Animal Behaviour* 62:1151-1162.
- McGarigal, K., S. Cushman, and S. Stafford. 2000. *Multivariate Statistics for Wildlife and Ecology Research*. Springer, New York, New York, USA.

- McShane, L. J., J. A. Estes, M. L. Riedman, and M. M. Staedler. 1995. Repertoire, structure, and individual variation of vocalizations in the sea otter. *Journal of Mammalogy* 76:414-427.
- Mitani, J. C., and J. Gros-Louis. 1995. Species and sex-differences in the screams of chimpanzees and bonobos. *International Journal of Primatology* 16:393-411.
- Naguib, M., and R. H. Wiley. 2001. Estimating the distance to a source of sound: mechanisms and adaptations for long-range communication. *Animal Behaviour* 62:825-837.
- Nass, R. D. 1977. Mortality associated with sheep operations in Idaho. *Journal of Range Management* 30:253-257.
- , 1980. Efficacy of predator damage control programs. *Proceedings of the Vertebrate Pest Conference* 9:205-208.
- National Agricultural Statistics Service. 1996. Cattle predator loss. U.S. Department of Agriculture, Washington, D.C., USA.
- , 2000a. Cattle. United States Department of Agriculture, Washington, D.C., USA.
- , 2000b. Sheep and goats. United States Department of Agriculture, Washington, D.C., USA.
- , 2000c. Sheep and goats predator loss. United States Department of Agriculture, Washington, D.C., USA.
- , 2001. Cattle predator loss. United States Department of Agriculture, Washington, D.C., USA.
- , 2003. Agricultural Statistics 2003. United States Department of Agriculture, Washington, D.C., USA.

- Nowak, R. M. 1999. Walker's Mammals of the World. 6th edition. Johns Hopkins University Press, Baltimore, Maryland, USA.
- O'Gara, B. W., K. C. Brawley, J. R. Munoz, and D. R. Henne. 1983. Predation on domestic sheep on a western Montana ranch. *Wildlife Society Bulletin* 11:253-264.
- Okanoya, K., and T. Kimura. 1993. Acoustical and perceptual structures of sexually dimorphic distance calls in Bengalese Finches (*Lonchura striata domestica*). *Journal of Comparative Psychology* 107:386-394.
- Okoniewski, J. C., and R. E. Chambers. 1984. Coyote vocal response to an electronic siren and human howling. *Journal of Wildlife Management* 28:217-222.
- Olsen, A., and P. N. Lehner. 1978. Conditioned avoidance of prey in coyotes. *Journal of Wildlife Management* 42:676-679.
- Owren, M. J., and D. Rendall. 2001. Sound on the rebound: Bringing form and function back to the forefront in understanding nonhuman primate vocal signaling. *Evolutionary Anthropology* 10:58-71.
- Peake, T. M., P. K. McGregor, K. W. Smith, G. Tyler, G. Gilbert, and R. E. Green. 1998. Individuality in corncrake *Crex crex* vocalizations. *Ibis* 140:120-127.
- Pearson, E. W., and M. Caroline. 1981. Predator control in relation to livestock losses in central Texas. *Journal of Range Management* 34:435-441.
- Phillips, A. V., and I. Stirling. 2000. Vocal individuality in mother and pup South American fur seals, *Arctocephalus australis*. *Marine Mammal Science* 16:592-616.

- Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pages 65-110 *in* L. Boitani, and T. K. Fuller, editors. Research Techniques in Animal Ecology. Columbia University Press, New York, New York, USA.
- Pye, J. D., and W. R. Langbauer, Jr. 1998. Ultrasound and infrasound. Pages 221-250 *in* S. L. Hopp et al., editors. Animal Acoustic Communication. Springer-Verlag, New York, New York, USA.
- Reby, D., B. Cargnelutti, E. Joachim, and S. Aulagnier. 1999. Spectral acoustic structure of barking in roe deer (*Capreolus capreolus*). Sex-, age- and individual-related variations. Comptes Rendus de l'Académie des Sciences Serie III - Sciences de la Vie 322:271-279.
- Riede, T., and T. Fitch. 1999. Vocal tract length and acoustics of vocalization in the domestic dog (*Canis familiaris*). Journal of Experimental Biology 202:2859-2867.
- Riede, T., H. Herzog, K. Hammerschmidt, L. Brunnberg, and G. Tembrock. 2001. The harmonic-to-noise ratio applied to dog barks. Journal of the Acoustical Society of America 110:2191-2197.
- Robel, R. J., A. D. Dayton, F. R. Henderson, R. L. Meduna, and C. W. Spaeth. 1981. Relationships between husbandry methods and sheep losses to canine predators. Journal of Wildlife Management 45:894-911.
- Rubin, P., and E. Vatikiotis-Bateson. 1998. Measuring and modeling speech production. *in* S. L. Hopp et al., editors. Animal Acoustic Communication. Springer-Verlag, New York, New York, USA.

- Sacks, B. N., K. M. Blejwas, and M. M. Jaeger. 1999a. Relative vulnerability of coyotes to removal methods on a northern California ranch. *Journal of Wildlife Management* 63:939-949.
- Sacks, B. N., M. M. Jaeger, J. C. C. Neale, and D. R. McCullough. 1999b. Territoriality and breeding status of coyotes relative to sheep predation. *Journal of Wildlife Management* 63:593-605.
- Sayigh, L. S., P. L. Tyack, R. S. Wells, A. R. Solow, M. D. Scott, and A. B. Irvine. 1999. Individual recognition in wild bottlenose dolphins: a field test using playback experiments. *Animal Behaviour* 57:41-50.
- Seaman, D. E., B. Griffith, and R. A. Powell. 1998. KERNELHR: A program for estimating animal home ranges. *Wildlife Society Bulletin* 26:95-100.
- Seaman, D. E., J. J. Millspaugh, B. J. Kernohan, G. C. Brundige, K. J. Raedeke, and R. A. Gitzen. 1999. Effects of sample size on kernel home range estimates. *Journal of Wildlife Management* 63:739-747.
- Selvin, S. 1995. *Practical Biostatistical Methods*. 1st edition. Duxbury Press, Belmont, California, USA.
- Shivik, J. A., and D. J. Martin. 2000. Aversive and disruptive stimulus applications for managing predation. *Proceedings of the Wildlife Damage Management Conference* 9:111-119.
- Stoddart, L. C., R. E. Griffiths, and F. F. Knowlton. 2001. Coyote responses to changing jackrabbit abundance affect sheep predation. *Journal of Range Management* 54:15-20.



- Theberge, J. B., and J. B. Falls. 1967. Howling as a means of communication in timber wolves. *American Zoologist* 7:331-338.
- Tigner, J. R., and G. E. Larson. 1977. Sheep losses on selected ranches in southern Wyoming. *Journal of Range Management* 30:244-252.
- Till, J. A., and F. F. Knowlton. 1983. Efficacy of denning in alleviating coyote depredations upon domestic sheep. *Journal of Wildlife Management* 47:1018-1025.
- Timm, R. M., and G. E. Connolly. 2001. Sheep-killing coyotes a continuing dilemma for ranchers. *California Agriculture* 55:26-31.
- Titus, K., J. A. Mosher, and B. K. Williams. 1984. Chance-corrected classification for use in discriminant analysis: ecological applications. *American Midland Naturalist* 111:1-7.
- Tooze, Z. J., F. H. Harrington, and J. C. Fentress. 1990. Individually distinct vocalizations in timber wolves, *Canis lupus*. *Animal Behaviour* 40:723-730.
- United States International Trade Commission. 2002. Lamb meat: evaluation of the effectiveness of import relief. Report number 3512. United States International Trade Commission, Washington, D.C., USA.
- Vicario, D. S., N. H. Naqvi, and J. N. Raksin. 2001. Sex differences in discrimination of vocal communication signals in a songbird. *Animal Behaviour* 61:805-817.
- Volodin, I. A., and E. V. Volodina. 2002. Biphonation as a prominent feature of dhole *Cuon alpinus* sounds. *Bioacoustics* 13:105-120.
- Wade, D. A. 1976. The use of aircraft in predator control. *Proceedings of the Vertebrate Pest Conference* 7:154-160.

- Wade, D. A., and J. E. Bowns. 1982. Procedures for evaluating predation on livestock and wildlife. Texas Agricultural Extension Service, Texas Agricultural Experiment Station, and Texas A&M University, College Station, Texas, USA.
- Wagner, F. H. 1988. Predator control and the sheep industry: The role of science in policy formation. Regina Books, Claremont, California, USA.
- Wagner, K. K. 1997. Preventative predation management: An evaluation using winter aerial coyote hunting in Utah and Idaho. Dissertation, Utah State University, Logan, Utah, USA.
- Wagner, K. K., and M. R. Conover. 1999. Effect of preventive coyote hunting on sheep losses to coyote predation. *Journal of Wildlife Management* 63:606-612.
- Walcott, C., D. Evers, M. Froehler, and A. Krakauer. 1999. Individuality in "yodel" calls recorded from a banded population of common loons, *Gavia immer*. *Bioacoustics* 10:101-114.
- Walsh, P. B., and J. M. Inglis. 1989. Seasonal and diel rate of spontaneous vocalization in coyotes in south Texas. *Journal of Mammalogy* 70:169-171.
- Weiss, D. J., B. T. Garibaldi, and M. D. Hauser. 2001. The production and perception of long calls by cotton-top tamarins (*Saguinus oedipus*): Acoustic analyses and playback experiments. *Journal of Comparative Psychology* 115:258-271.
- Wiley, R. H., and D. G. Richards. 1978. Physical constraints on acoustic communication in the atmosphere: Implications for the evolution of animal vocalizations. *Behavioral Ecology and Sociobiology* 3:69-94.

- Williams, C. L., K. Blejwas, J. J. Johnston, and M. M. Jaeger. 2003. A coyote in sheep's clothing: predator identification from saliva. *Wildlife Society Bulletin* 31:926-932.
- Windberg, L. A., and F. F. Knowlton. 1990. Relative vulnerability of coyotes to some capture procedures. *Wildlife Society Bulletin* 18:282-290.
- Wolfe, G. J. 1974. Siren-elicited howling response as a coyote census technique. Thesis, Colorado State University, Fort Collins, Colorado, USA.
- Zar, J. H. 1999. *Biostatistical Analysis*. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.