

Acoustic structures in the alarm calls of Gunnison's prairie dogs

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Acoustic structures of sound in Gunnison's prairie dog alarm calls are described, showing how these acoustic structures may encode information about three different predator species (red-tailed hawk—*Buteo jamaicensis*; domestic dog—*Canis familiaris*; and coyote—*Canis latrans*). By dividing each alarm call into 25 equal-sized partitions and using resonant frequencies within each partition, commonly occurring acoustic structures were identified as components of alarm calls for the three predators. Although most of the acoustic structures appeared in alarm calls elicited by all three predator species, the frequency of occurrence of these acoustic structures varied among the alarm calls for the different predators, suggesting that these structures encode identifying information for each of the predators. A classification analysis of alarm calls elicited by each of the three predators showed that acoustic structures could correctly classify 67% of the calls elicited by domestic dogs, 73% of the calls elicited by coyotes, and 99% of the calls elicited by red-tailed hawks. The different distributions of acoustic structures associated with alarm calls for the three predator species suggest a duality of function, one of the design elements of language listed by Hockett [in *Animal Sounds and Communication*, edited by W. E. Lanyon and W. N. Tavolga (American Institute of Biological Sciences, Washington, DC, 1960), pp. 392–430]. © 2006 Acoustical Society of America. [DOI: 10.1121/1.2185489]

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I. INTRODUCTION

The alarm calls of some animals have been shown to have referential meaning. These calls refer to something in the external environment of the animal, such as a predator, that elicits an alarm response. A number of animals have calls for terrestrial and for aerial predators. These animals include many ground squirrels (*Spermophilus spp*) (Owings and Hennessy, 1984), chickens (*Gallus gallus domesticus*) (Evans and Evans, 1999), tree squirrels (*Tamiasciurus hudsonicus*) (Greene and Meagher, 1998), dwarf mongooses (*Helogale undulata*) (Beynon and Rasa, 1989), and suricates (*Suricata suricatta*) (Manser, 2001; Manser *et al.*, 2001). In each of these species, a terrestrial predator elicits an acoustically different alarm call from that elicited by an aerial predator. A few animal species have been shown to have specific vocalizations for different predator species or categories of predators. Such referential meaning has been documented for vervet monkeys (*Cercopithecus aethiops*), Diana monkeys (*Cercopithecus diana*), Campbell's monkeys (*Cercopithecus campbelli*), and prairie dogs (*Cynomys gunnisoni*). Vervet monkeys have calls for three different types of predators: snake or python, leopard, and eagle (Cheney and Seyfarth, 1990). Diana monkeys and Campbell's monkeys have calls for leopards (*Panthera pardus*) and crowned-hawk eagles (*Stephanoaetus coronatus*) (Zuberbuhler, 2000, 2001).

Gunnison's prairie dogs, which are found in the grasslands of northern Arizona, northern New Mexico, southern Colorado, and eastern Utah, have alarm calls for four different species of predator: hawk (*Buteo jamaicensis*), human (*Homo sapiens*), coyote (*Canis latrans*), and domestic dog (*Canis familiaris*) (Placer and Slobodchikoff, 2000, 2001), as well as vocalizations for objects in their environment that are not known to them but could potentially represent a predator (Ackers and Slobodchikoff, 1999). The escape responses of the prairie dogs differ to the different predators (Kiriazis, 1991; Slobodchikoff, 2002; Kiriazis and Slobodchikoff, 2006). When a human appears at the edge of the colony, all of the prairie dogs run to their burrows and dive inside. When a red-tailed hawk dives toward the colony in an attempt to capture a prairie dog, only the animals in the immediate flight path of the hawk run to their burrows and dive inside. The remaining animals outside the flight path typically stand on their hind legs and watch the progress of the hawk. When a coyote appears, all the animals in the colony run to the lips of their burrows and stand upright in an alert posture, and prairie dogs that are below ground emerge to stand at their burrows so that most of the colony is above ground, watching the coyote. When a domestic dog appears, the prairie dogs stand in an alert posture, and only run to their burrows if the dog comes near. In playback experiments, Kiriazis and Slobodchikoff (2006) showed that the escape responses of the prairie dogs to playbacks of the calls for the different predators when no predator is present are the same as when a predator appears and elicits alarm calls and escape responses from the animals in the colony. Of these four predators, humans represent perhaps the greatest threat,

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shooting large numbers of prairie dogs (Vosburgh and Irby, 1998). Coyotes and hawks are responsible for the majority of nonhuman predation, while domestic dogs seem to represent relatively little threat as predators (Verdolin and Slobodchikoff, 2002).

In addition to containing information about the species of predator, Gunnison's prairie dog alarm vocalizations also provide information about specific details of an individual predator. Slobodchikoff *et al.* (1991) found that Gunnison's prairie dogs incorporated information into their calls about specific colors of shirts, such as blue, green, yellow, and grey, worn by different humans, and also found that the calls incorporated details of the size and shape of the individual humans. When Slobodchikoff *et al.* (1991) had humans of different sizes and shapes walking through prairie dog colonies wearing the same white laboratory coat that obscured physical features, the prairie dogs incorporated less information into their alarm calls about the individual humans than when the humans were not wearing the laboratory coat. A recent study has shown that the other four species of prairie dogs in North America (the black-tailed, *Cynomys ludovicianus*, found in the western part of the Midwest; the Mexican, *C. mexicanus*, found in central Mexico; the white-tailed, *C. leucurus*, found in western Colorado and northeastern Utah; and the Utah, *C. parvidens*, found in southwestern Utah) can also incorporate information into their alarm calls about different shirt colors worn by humans (Frederiksen, 2005). The calling patterns of the Gunnison's prairie dogs differ depending on whether a predator is approaching slowly or rapidly, providing the prairie dogs with a wide range of information about the species of predator, the individual characteristics or description, and the rate of approach (Kiriazis, 1991; Slobodchikoff, 2002). This represents a complex communication system that appears to exceed the amount of information encoded in the calls of many other species with referential labeling.

In earlier studies (Placer and Slobodchikoff, 2000, 2001) an artificial neural network was used to classify Gunnison's prairie dog alarm calls by species of predator. Each alarm call was decomposed into several equal-sized time periods and the ratios of the frequencies present in each period were computed. The frequency ratios in all time periods for a given alarm call were then combined to represent that alarm call. This measure of frequency ratios was used as input to a neural network. The classification results clearly showed that frequency ratios could be used to classify predator-specific prairie dog alarm calls. However, although high classification accuracy was achieved in that study, the frequency ratios did not retain time-dependent information nor did they provide information about the underlying acoustic structure of the calls.

Analysis of the acoustic structure of such alarm calls in mammals has most often focused on a description of the sound frequencies and time-dependent parameters of those frequencies. For example, the alarm calls of vervet monkeys (*Cercopithecus aethiops*) and rhesus macaques (*Macaca mulatta*) have been analyzed in terms of the fundamental frequencies (F_0) (Hauser and Fowler, 1992), and vervet monkeys (Seyfarth and Cheney, 1984; Owren and Bernacki,

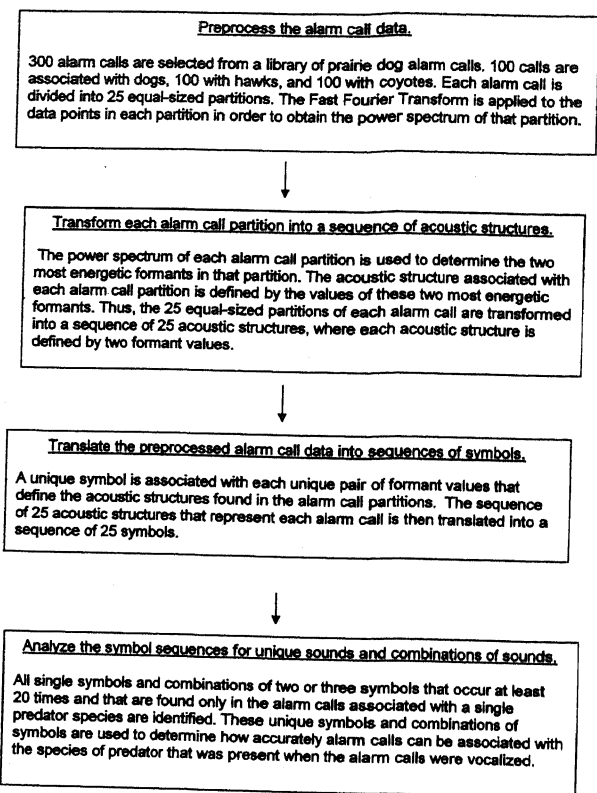


FIG. 1. Summary of the methods used in the analysis.

1988), Barbary macaques (*Macaca sylvanus*) (Fischer *et al.*, 1995), baboons (*Papio cynocephalus*) (Owren *et al.*, 1997; Fischer *et al.*, 2002), and Diana monkeys (*Cercopithecus diana*) (Riede and Zuberbühler, 2003) have been analyzed in terms of frequency, time, and amplitude parameters. These analyses have not searched for deeper acoustic structures within the alarm calls.

II. METHODS

The methods that produced the research discussed in this paper are described in detail in Placer and Slobodchikoff (2004) and are summarized in Fig. 1. Three hundred (300) Gunnison's prairie dog alarm calls were selected from a large collection of tape recordings obtained over a 10-year period (1988–1997) at two separate prairie dog colonies described in Slobodchikoff *et al.* (1991). Details about this database can be found in Placer and Slobodchikoff (2004). One hundred (100) calls were vocalized in the presence of dogs, 100 in the presence of hawks, and 100 in the presence of coyotes. The alarm calls were converted into simple digitized time-domain recordings and processed to reduce background noise using the software package Cool Edit 2000. One of the authors (JP) created a system of computer programs to analyze these alarm calls using the high-performance numeric computation software called MATLAB and the computer language Java.

Each of the digitized alarm calls was divided into 25 equal-sized partitions. Figure 2 shows a digitized alarm call that has been divided into 25 partitions. The mean total times of the calls for the different predators were as follows: coyote: 0.193 ± 0.014 s (mean \pm SD), $N=100$ calls; dog:

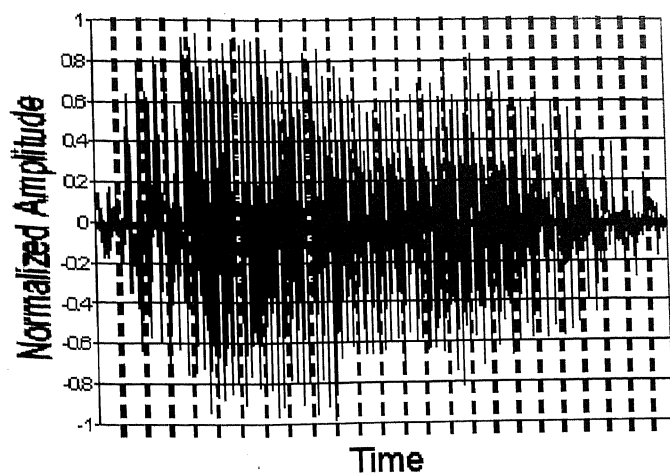


FIG. 2. A prairie dog call divided into 25 partitions.

O. 0.134 ± 0.020 s, $N=100$ calls; hawk: 0.084 ± 0.007 s, $N=100$. The mean times of the individual partitions were the following. Coyote: 0.0148 ± 0.003 s (mean \pm SD), $N=2500$ partitions; dog: 0.0103 ± 0.0015 s, $N=2500$ partitions; hawk: 0.0065 ± 0.0005 s, $N=2500$ partitions.

The fast fourier transform was then applied to the data points in each alarm call partition in order to produce a normalized power spectrum of the sound frequencies contained in that partition. The computer analysis software then used the eight most energetic frequencies of each power spectrum to determine the two most prominent formants (designated $F1$ and $F2$) contained in that alarm call partition, where formant values were rounded to the nearest multiple of 300 Hz. Figure 3 shows a typical power spectrum taken from one partition of a divided alarm call. The eight data points that lie above the horizontal line in the figure are the largest power values that are used to compute the two most energetic formants in this partition. The power values that are clustered together as contiguous data points are treated as part of a single formant. The lowest frequency in such a cluster is used to represent that formant. Formants are vocal tract resonances that appear as hills or raised sections in a power spec-

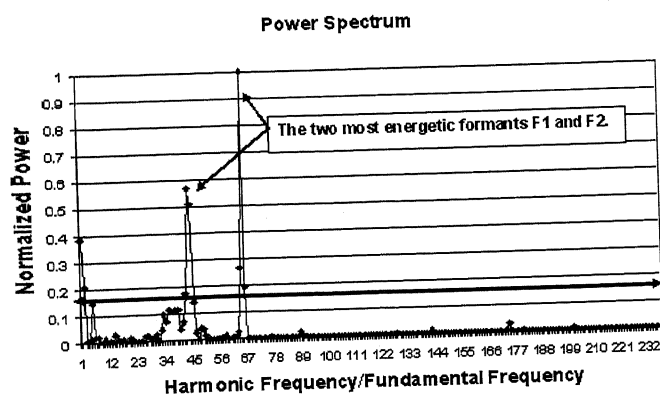


FIG. 3. The power spectrum of a partition of a prairie dog alarm call vocalized in the presence of a hawk. The two most energetic formants were used to identify distinct acoustic units. The values on the vertical axis are normalized because the absolute values of the power are not relevant. The values on the horizontal axis represent an index expressed in simple integers, derived by dividing the harmonic frequencies in the power spectrum of the partition by the fundamental frequency in that partition.

TABLE I. Sound frequency values (Hz) for the most common acoustic structures associated with alarm calls for coyotes.

Symbol No.	F1	F2
S6	0	3600
S15	0	3900
S13	300	3600
S14	300	3900
S31	300	4200
S17	300	3300
S23	300	600
S32	300	900
S62	2700	3600
S61	2700	3300
S16	3000	3900
S60	3000	3600
S5	3300	3900
S3	3300	4200
S11	3300	3600
S7	3600	3900
S8	3600	4500
S4	3600	4200
S12	3900	4200

trum. A number of techniques for identifying the highest or most prominent formants were experimented with and the simple technique of using only the eight most energetic frequencies in each power spectrum produced the best results (Placer and Slobodchikoff, 2004).

Each of the two formants computed for each alarm call partition was represented by a single sound frequency. Thus, the acoustic structure associated with each partition was defined by two frequencies that represented that partition's two most energetic formants. Using this procedure, each alarm call would be divided into 25 equal-sized partitions and each partition in turn would be represented by two formant frequencies. In this way, each of the 300 alarm calls used in this study was translated into a sequence of 25 acoustic structures where each acoustic structure was represented by two simple frequencies (see Tables I–III).

Working with these translated alarm calls, the analysis software examined each acoustic structure in each alarm call. Each unique pair of frequencies that defined an acoustic unit

TABLE II. Sound frequency values (Hz) for the most common acoustic structures associated with alarm calls for domestic dogs.

Symbol No.	F1	F2
S47	300	1200
S32	300	900
S53	300	2700
S75	1200	3300
S120	1200	2400
S55	1200	3600
S3	3300	4200
S19	3300	4500
S5	3300	3900
S8	3600	4500
S18	3900	4800
S30	4200	5100

TABLE III. Sound frequency values (Hz) for the most common acoustic structures associated with alarm calls for red-tailed hawks.

Symbol No.	F1	F2
S13	300	3600
S32	300	900
S14	300	3900
S17	300	3300
S23	300	600
S24	600	3600
S39	600	3300
S62	2700	3600
S61	2700	3300
S162	3000	6000
S68	3300	6300
S70	3300	6000
S143	3600	5700
S157	3600	5400
S71	3600	6300
S154	3900	5700
S2	3900	6000
S144	4200	6000
S155	5100	6000
S161	5100	6300
S153	5400	6300

was assigned a unique symbol and that symbol was used to replace the acoustic unit. For example, assume the acoustic unit (300 Hz, 600 Hz) was encountered during this phase of the processing. If that exact pair of frequencies had been encountered previously, then a symbol would already have been used to represent them and that symbol would be used to replace the pair of frequencies. However, if this was the first time that particular pair of frequencies was encountered, a new symbol would be generated and the new symbol would be used to replace the pair. The names of the symbols

always began with an "S" that was followed by a simple integer. Thus, if a new symbol was to be created and 25 symbols had already been generated, then the new symbol's name would be "S26." Using these techniques the alarm calls that had been translated into sequences of acoustic units were now translated into sequences of symbols. Shown below is an example of an alarm call vocalized in the presence of a coyote that has been translated into a sequence of 25 symbols:

S14S7S6S17S5S4S9S13S18S9S8S19S4S7S8S4S7
S6S6S4S19S4S19S8S13

Once the alarm calls were translated into sequences of symbols, the sequences were then searched for single symbols (monograms), pairs of contiguous symbols (digrams), and triplets of contiguous symbols (trigrams) that were found exclusively in the alarm calls associated with a particular predator species. Alarm calls found to contain a monogram, digram, or trigram that was uniquely associated with a given predator species could be unambiguously associated with that same predator species. Thus, monograms, digrams, and trigrams unique to a given predator species were used to classify the alarm calls by predator species. Only symbols that occurred at least 20 times in the target alarm calls were used in the classification process in order to guard against using infrequently occurring acoustic units that might simply be artifacts of the sound processing techniques utilized. Only symbols that occurred at least 50 times were considered to be common symbols that are used in the descriptions of the results below.

A similarity index was calculated based on counts of occurrence of the different acoustic symbols within the three types of calls. The index was calculated as

$$\text{similarity index} = \sum \frac{A \text{ or } B \text{ (whichever has the smaller number of occurrences)}}{A + B}$$

where *A* is the frequency of occurrence of a symbol in the calls elicited by one predator, *B* is the frequency of occurrence of the same symbol in the calls elicited by the other predator, and the index is summed over all of the symbols that are common to the calls of both predators.

III. RESULTS

Most of the common acoustic structures (>50 occurrences) were found in calls associated with all three predators, but the proportions of acoustic structures varied. In alarm calls elicited by coyotes, there was only a single acoustic structure (S15) that was unique to coyote calls (Fig. 4). In alarm calls elicited by domestic dogs, there was also

only one acoustic structure (S120) that was unique (Fig. 5). In alarm calls elicited by red-tailed hawks, there were six acoustic structures (S153, S154, S155, S157, S161, and S162) that were unique to red-tailed hawk calls (Fig. 6). The proportion of occurrence of the symbols in the three types of calls was significantly different (coyote-hawk, $\chi^2=1770/2$ (Bonferroni correction)=885, *df*=23, *p*<0.001; hawk-dog, $\chi^2=1374/2$ (Bonferroni correction)=687, *df*=22, *p*<0.001; coyote-dog, $\chi^2=679/2$ (Bonferroni correction)=340, *df*=19, *p*<0.001; χ^2 values were calculated on the basis of counts of occurrences). Based on the occurrence of acoustic structures in the calls, hawk calls and coyote calls had a similarity of 0.159, hawk calls and dog calls had a similarity of 0.134, and coyote calls and dog calls had a similarity of 0.218.

COMMONEST COYOTE SYMBOLS

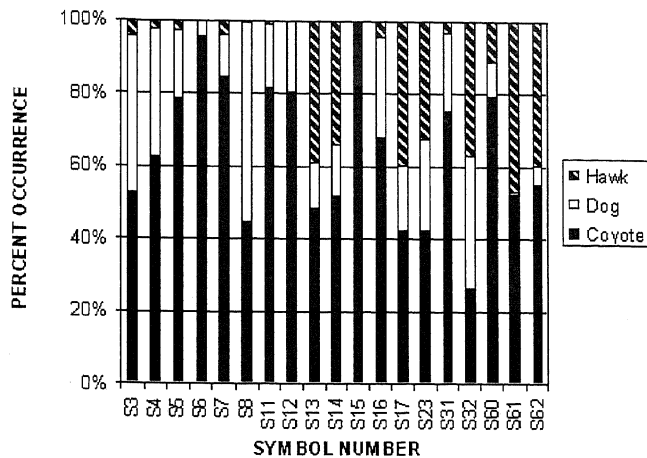


FIG. 4. The most common acoustic structures found within calls elicited by coyotes. Only one acoustic structure (S15) is unique to coyote calls.

When digrams and trigrams were considered, there were more unique combinations. A number of these consisted of repetition of the same acoustic structure in contiguous partitions. Dog elicited calls had a unique trigram consisting of the same acoustic structure (S120) repeated in three adjacent partitions (S120S120S120), and another unique trigram consisting of an acoustic structure (S47) also repeated in three adjacent partitions (S47S47S47). Coyote elicited calls had three unique digrams and two unique trigrams. Of the digrams, one consisted of repetition of the same acoustic structure in two adjacent partitions (S6S6), and two consisted of two different acoustic structures in adjacent partitions (S16S60; S7S6). The two unique trigrams in coyote elicited calls were repetitions of the same acoustic structures in three adjacent partitions (S5S5S5; S7S7S7). Hawk elicited calls had eight unique digrams and one unique trigram. Of these, three consisted of repetitions of the same acoustic structures in adjacent partitions (S68S68; S70S70; S154S154), and five consisted of associations of different acoustic structures in

COMMONEST DOG SYMBOLS

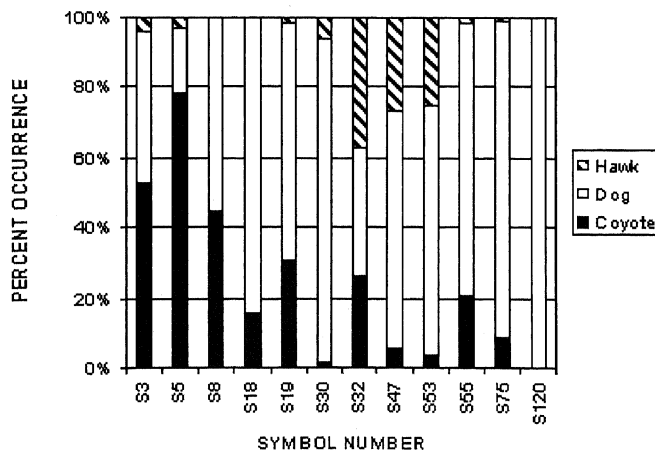


FIG. 5. The most common acoustic structures found within calls elicited by domestic dogs. Only one acoustic structure (S120) is unique to domestic dog calls.

COMMONEST HAWK SYMBOLS

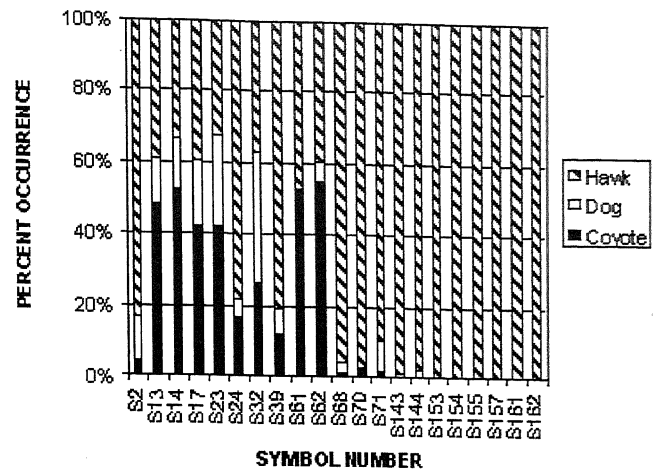


FIG. 6. The most common acoustic structures found within calls elicited by red-tailed hawks. Six acoustic structures (S153, S154, S155, S157, S161, S162) are unique to red-tailed hawk calls.

adjacent partitions (S2S154; S68S70; S70S68; S154S157; S154S143). The unique trigram in hawk elicited calls consisted of a repetition of the same acoustic structure (S68) in three adjacent partitions (S68S68S68).

Using the unique monograms, digrams, and trigrams, we subjected the original data to a classification analysis to determine how well these unique acoustic structures can identify the calls to the correct predator species. We found that 67% of the dog elicited calls were correctly classified as dog, 73% of the coyote elicited calls were correctly classified as coyote, and 99% of red-tailed hawk elicited calls were correctly classified as hawk, giving an overall classification average of 80% correct classification. When we plotted all of the acoustic structures that made up the unique monograms, digrams, and trigrams, we found that the acoustic structures associated with these unique grams for each predator species seemed to cluster in different regions (Fig. 7). Hawk-associated acoustic structures generally had higher formant frequencies for both $F1$ and $F2$ than the coyote- or domestic dog-associated frequencies, which had lower formant frequencies.

When we ranked the acoustic structures by ascending $F1$ frequency (Figs. 8–10), the acoustic structures produced a pattern in which the higher formant frequency increased in one symbol and then decreased in the following symbol for many of the symbols. This is a pattern similar to that seen in the structure of English vowels when the two lowest formants associated with each vowel are plotted (Fig. 11) [source of frequencies for English vowels (Kim, 1991)].

IV. DISCUSSION AND CONCLUSIONS

The same acoustic structures were found in calls associated with all three species of predator. However, the distribution of these acoustic structures was different for each of the three predators. This suggests two points. One is that the acoustic structures could be used as building blocks for larger units that might have meaning, in a way analogous to how phonemes are used in human languages to build words

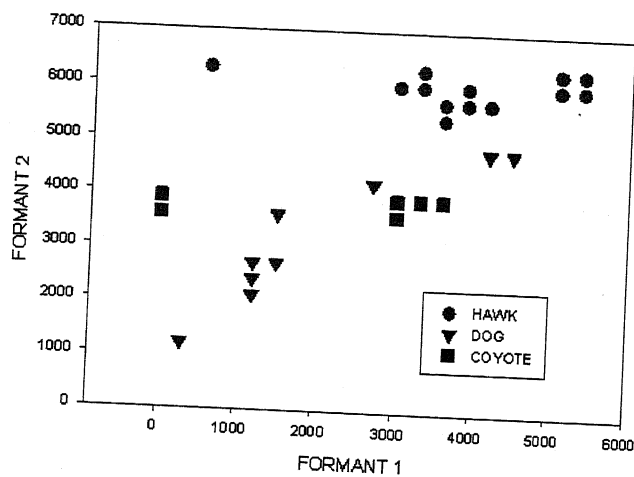


FIG. 7. Formant frequencies found in unique monograms, digrams, and trigrams associated with red-tailed hawk, coyote, and domestic dog alarm calls. The F1 and F2 frequency (Hz) values for each symbol that is part of a unique combination have been plotted, even though that symbol may be part of a unique digram or a unique trigram.

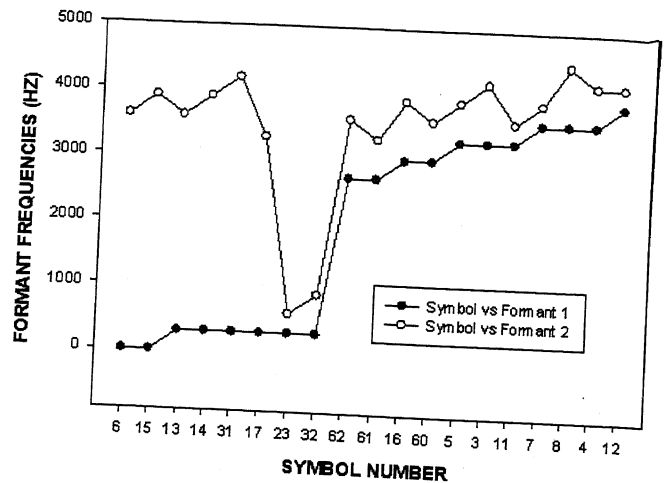


FIG. 9. Formant frequencies for calls elicited by coyotes, with the lower frequency ascending.

and sentences. This suggests that prairie dog alarm vocalizations might contain duality, i.e., that larger units of semantic significance are made up of smaller units that can be combined in different ways to produce many different larger units. This is one of the design features of language listed by Hockett (1960) for human and animal languages and has not been shown previously in animal vocalizations. The other point is that perhaps some or many acoustic structures might be used to express additional information beyond the species of predator present when an alarm call is vocalized. This hypothesis is consistent with the work of Slobodchikoff *et al.* (1991), who demonstrated that prairie dog calls contain information associated with size, shape, and color of different individuals within a predator species, and it is consistent with the work of Kiriazis (1991), who showed that prairie dog calls contain information related to direction and speed of approach of predators.

The vowel-like acoustic structures in prairie dog alarm calls are perhaps not surprising, given that at least one non-

human primate, the baboon (*Papio cyncephalus*), is known to produce grunts that have acoustic properties similar to those of human vowels (Zhinkin, 1963; Andrew, 1976; Owren *et al.*, 1997). Also, other animals have been found to be able to discriminate among some human vowels. For example, cats (Dewson, 1964), chinchillas (Miller, 1977), baboons (Hienz and Brady, 1988), and pigeons (Hienz *et al.*, 1981) have been shown to be able to discriminate between some of the human vowels. Among the nonhuman primates, vervet monkeys (*Cercopithecus aethiops*) and Japanese macaques (*Macaca fuscata*) were able to discriminate between some of the common English vowels (Sinnott, 1989). Perhaps there is a limited number of ways in which information might be encoded in vocalizations that have multiple formants. However, we should point out that the duration of English vowels varies between 0.180 and 0.330 s (Lieberman and Blumstein, 1988), while the acoustic structures that we have identified vary between 0.0065 and 0.0148 s in du-

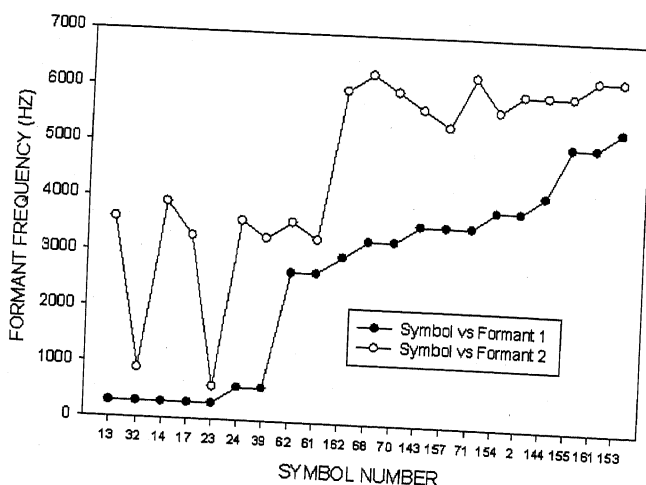


FIG. 8. Formant frequencies for calls elicited by red-tailed hawks, with the lower frequency ascending.

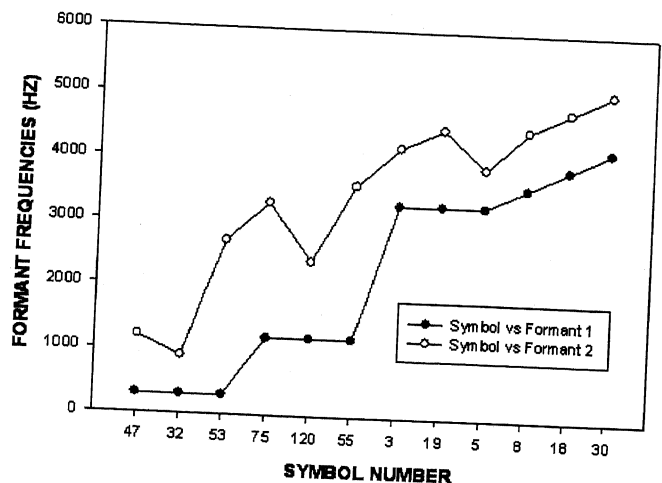


FIG. 10. Formant frequencies for calls elicited by domestic dogs, with the lower frequency ascending.

ENGLISH VOWEL SOUNDS

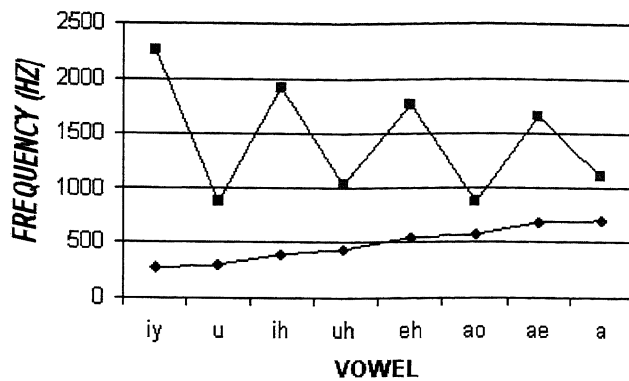


FIG. 11. Frequencies (Hz) for eight American English vowels, showing the lower frequency (F1) and the higher frequency (F2) for each vowel. The vowel symbols stand for the following: iy as in "beet," u as in "put," ih as in "bit," uh as in "Buddhist," eh as in "met," ao as in "cause," ae as in "bad," and a as in "cat." Sound frequencies of vowels from Kim (1991).

ration. Since the entire alarm calls of the prairie dogs vary between 0.084 and 0.193 s in duration and there is a considerable amount of information encoded within that total time interval, it is possible that prairie dogs might process acoustic information more rapidly than humans.

Somewhat more surprising is the acoustic structure of these vowel-like sounds. In humans and other primates, vowel-like sounds are produced through a combination of the first two formants, that is, the two formants with the lowest frequencies (Owren *et al.*, 1997). In prairie dog alarm vocalizations, the most accurate associations of alarm calls with predator species occurred when the two most dominant formants, the ones carrying the most acoustic energy, were used, rather than the first two. Perhaps this is an adaptation to the long-distance propagation of sound in the alarm call, since prairie dog calls travel over long distances, often through vegetation that can potentially filter out some frequencies (e.g., see Perla and Slobodchikoff, 2002).

ACKNOWLEDGMENTS

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