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Communication of Stimulus Size and Shape in Alarm Calls of Gunnison's Prairie Dogs, *Cynomys gunnisoni*

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Abstract

Gunnison's prairie dogs (*Cynomys gunnisoni*) emit multiple-note alarm calls to terrestrial predators that vary in acoustic structure according to the eliciting stimulus. The characteristics of the predator that are salient with respect to alarm call variation, however, are poorly understood. Although the behavior of predators has been shown to influence alarm call production in other species of ground-dwelling sciurids, the degree to which sciurid alarm calls describe physical characteristics of predators has not been addressed independently of the effects of variation in predator behavior. The effect of variation in the size and shape of the eliciting stimulus was studied by presenting silhouette models to a colony of prairie dogs and recording the alarm calls that were elicited. Discriminant function analysis on 7 variables measured from spectrograms revealed that the alarm calls differed with respect to silhouette. These results suggest that information with respect to stimulus size and shape is encoded in prairie dog alarm calls.

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Introduction

Many species of vertebrates demonstrate the ability to adjust their response to predators according to the nature of the risk posed by a given predator category. Because variation in predation risk may encompass both behavioral and morphological characteristics of predators, prey species might be expected to categorize their predators along both behavioral and morphological dimensions. Given the type of predator and the predator's behavior, a potential prey might predict the future behavior of the predator allowing the prey to choose the response most likely to result in escape (see, e.g. Lima & Dill 1990).

One of the most common forms of vocal communication is the production of alarm calls in response to a predatory encounter. These calls are thought to promote the survival of genetic relatives by providing information about predation risk (e.g. Dunford 1977; Sherman 1977, 1980; Leger & Owings 1978; Hoogland 1983). Several species of birds and mammals produce multiple types of alarm calls that differ in spectral characteristics and are given in response to different classes

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of predators. Typically, the alarm calls are of two broad types: alarm calls usually elicited by aerial predators and alarm calls usually elicited by terrestrial predators (e.g. *Spermophilus beecheyi*–Owings & Virginia 1978; *Saimiri sciureus*–Jürgens 1979; Owings & Leger 1980; *Gallus gallus*–Gyger et al. 1987; *Vanellus* spp.–Walters 1990; *Marmota marmota*–Lenti Boero 1992). In alarm-calling systems consisting of two distinct types of calls, the calls appear to provide information about the behavior of the predator; single-note or short duration alarm calls appear to inform receivers of a more immediate threat than multiple-note or long duration alarm calls (see MacEdonia & Evans 1993 for a review). To some extent, this corresponds to aerial (immediate threat) and terrestrial (distant threat) predators although the two call types are often not completely production-specific and probably convey more information about response urgency than about predator type (e.g. Blumstein & Arnold 1995; Blumstein & Armitage 1997).

Alarm calls produced by vervet monkeys (*Cercopithecus aethiops*) in response to three different classes of predators show considerably greater production specificity corresponding to a combination of physical and behavioral characteristics of vervet predators (Struhsaker 1967; Seyfarth et al. 1980). Experiments with silhouette models of predators have shown that vervet alarm calls begin to grade into one another when behavioral information and some of the morphological cues are excluded from the eliciting stimulus (Brown et al. 1992). The remaining morphological characteristics of predators provided by the silhouettes were sufficient to produce differences in the acoustic structure of the alarm calls although the absence of behavioral cues probably contributed to the intergradation of the call types. Thus, the cues provided by the silhouettes were sufficient to produce differences among alarm calls to the different stimuli but did not produce complete production specificity.

In all of the above examples, the calls fall into a limited number of discrete categories and there is little overlap between call types when produced in response to actual predators. Despite observable variation in the physical characteristics of predators, variation within a call type is usually not quantitatively addressed. The question remains as to the degree that prey species may categorize the physical characteristics of the predator separately from predator behavior (e.g. the likelihood of imminent attack). Variation in the production of alarm calls provides an assay for analysing how an animal might form categories in the context of predator avoidance.

In response to terrestrial predators, Gunnison's prairie dogs (*Cynomys gunnisoni*) emit multiple-note alarm calls consisting of a series of short bark-like vocalizations each ≈ 0.1 s in duration and repeated at 0.1–0.15 s intervals within an alarm call. Each alarm call typically consists of from 10 to over 100 barks with very little variation among the barks within an alarm call. A given prairie dog may emit one to several alarm calls during any one predatory encounter (Waring 1970). The tendency to alarm call varies among individuals and is probably related to the presence of genetic relatives or potential mates (Hoogland 1996).

Although there is evidence for production specificity between call structure and predator characteristics in Gunnison's prairie dog alarm calls (Slobodchikoff et al. 1986, 1991; Kiriazis 1991), variation in the behavior of a predator during natural encounters may affect the structure of prairie dog alarm calls in unknown ways. That is, we do not know the extent to which prairie dogs categorize their predators by behavior (i.e. hunting tactics) or physical characteristics. To address this difficulty, we constructed artificial models that were presented to individually marked prairie dogs under controlled conditions. Our objectives were to determine if variance in prairie dog alarm calls can be explained by differences in the size and shape of the eliciting stimuli and to evaluate which parameters of the alarm calls change in response to differences in the physical characteristics of the eliciting stimuli.

Methods

Study Site

We conducted the experiment at a prairie dog colony located in an undeveloped area within the city limits of Flagstaff, Arizona. A portion of the colony (0.63 km^2) was selected for study so that visual stimuli could be presented to a large number of animals while simultaneously recording their responses. All data were recorded from a tower blind (1.2 × 1.2 × 2.3 m) positioned on a small hill in the middle of the colony. The equipment was set up in the early morning (5.00–6.00h) prior to the daily emergence of the prairie dogs so that the observer could be hidden in the blind as the prairie dogs began foraging. The experiment was conducted after the emergence of the young of the year (late-May) when alarm calls are most easily elicited.

Subjects

We live-trapped 49 prairie dogs using Tomahawk model #204 live-traps and marked each animal with a numbered ear tag (Monel #1005 size 1) and Nyanzol D dye. The dye marks consisted of a letter and a number to indicate both individual identity and gender. Males were marked with the letters A–N while females were marked with the letters O–Z. After N9 and Z9 were marked, we reversed the order of the numbers and letters (i.e. 1A and 1O) to avoid giving the same mark to two different animals.

We weighed and classified each marked animal according to age (adult or juvenile) and sex. Each female was classified as breeding or nonbreeding based on whether the teats were enlarged. Seventeen juveniles and 32 adults were trapped. Sex ratios among the adults were 0.78 : 1 (males:females). Six of 18 (33%) adult females showed evidence of having bred.

Stimulus Presentations

We presented stimuli in the form of silhouette models to elicit alarm calls from the prairie dogs. This technique is a simple and effective means of eliciting alarm calls in controlled experiments (e.g. Tinbergen 1948; Brown et al. 1992). Three shapes of models were constructed of 0.64 cm thick plywood and coated with a nonreflective black paint: a coyote (a predator stimulus; 110 × 62.5 cm, 3163 cm²), a skunk (a nonpredator stimulus; 55 × 20 cm, 667 cm²), and an oval shape (a novel stimulus; 80.5 × 65 cm, 4110 cm²). The silhouettes were presented by placing a model on a stationary line and moving it via a second line attached to the model itself. The stationary line consisted of 50 m of braided nylon cord 3.2 mm in diameter stretched tightly between the observation blind and a tree or a fencepost and supported at 10 m intervals by wooden stakes 1 m in height. The models were presented to different groups of animals by changing the direction of this line. The model was shielded from view with two 1 × 1.5 m burlap screens prior to each trial, then during the trial it was pulled along the stationary line on two slotted wheels 2 cm in diameter with a second braided nylon cord 1.6 mm in diameter. The movement of the model was controlled by the observer and began with 10 m of movement at a rate of 2 m/s. The model was then paused for 60 s to allow the prairie dogs to notice its appearance and also to allow the observer to record which individuals produced alarm calls. After the pause, the model was again moved at the same rate for the same distance and then paused for another 60 s. This pattern of movement continued until the model reached the other end of the line. One presentation was conducted per day with the shape of model randomly determined. Alarm calls directed toward the model were recorded on audio tape using a Sennheiser ME-88 directional microphone connected to a Sony TC-D5PRO II cassette recorder. Only alarm calls from adult prairie dogs were used in the analysis.

Statistical Analyses

The first alarm call from the first animal that called during each trial was used for analysis. Spectrograms of each alarm call were produced using a RTS Real-Time Spectrogram package (Engineering Design, Belmont) installed in a IBM-compatible personal computer (486 processor; 33 MHz clock speed). Sample rate was set at 25 kHz with a frequency resolution of 48.8 Hz.

Each alarm call was partitioned into 1-s intervals prior to obtaining measurements from the spectrograph screen. Time and frequency coordinates were digitized from eight points on each bark within the call and then used to calculate seven dependent variables used in the statistical analyses: fundamental frequency, dominant frequency, supradominant frequency, interharmonic interval, duration, ascending slope, and descending slope (Fig. 1). These variables were selected to encompass variation in duration, frequency, the rate of frequency modulation, and harmonic structure. The mean standardized measurements of all of the barks in the first alarm call emitted during a silhouette presentation were calculated for each individual. Stepwise discriminant function analysis (SPSSx rel. 4.1) was used to determine if the calls differed with respect to silhouette shape and which of the variables contributed to the variance among calls with respect to silhouette shape. The method of minimizing Wilks' lambda was used as the stepping criterion. A classification matrix was produced for the mean call variables using prior probabilities based on the sample sizes for each treatment. The relative contribution of each of the original variables was assessed by examining the pooled within-groups

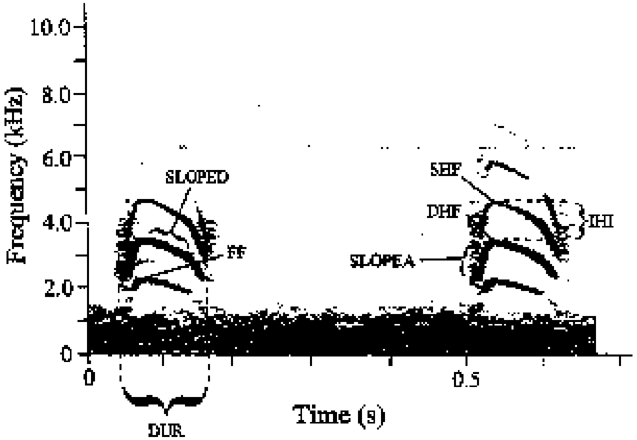

Fig. 1. A spectrogram of two prairie dog alarm barks produced in response to the coyote silhouette. Eight points were digitized from the spectrograph screen and used to calculate the variables used in the stepwise discriminant function analyses. The variables are abbreviated in the spectrogram as follows: DHF: dominant harmonic frequency (Hz), FF: fundamental frequency (Hz), SHF: supradominant frequency (Hz), IHI: interharmonic interval (Hz), DUR: duration (ms), SLOPEA: ascending slope (Hz/ms), SLOPED: descending slope (Hz/ms)

correlations between the original variables and the canonical variables (Norusis 1985).

We analysed call variation among the silhouette shapes within individuals by entering all of the barks into separate discriminant function analyses for each animal that provided calls to more than one silhouette. Inferential statistics are not reported for these analyses because the barks given by an individual within an alarm call recorded during a single trial clearly are not independent observations. Rather, the discriminant functions were used as a descriptive tool to illustrate graphically the differences among the calls given by an individual in response to different stimuli.

We analysed individual variation within the alarm calls to each silhouette shape by performing cluster analyses on the mean standardized call variables for each individual within each treatment. Squared Euclidean distances were used as a measure of the degree of individual variation within a treatment group. The centroid method was used to determine the pattern of clustering (Norusis 1985). Separate analyses were performed for the calls to each silhouette shape.

Results

The mean alarm call variables for the 15 prairie dogs that called differed with respect to silhouette shape (Fig. 2; Wilks' lambda (4, 2, 12) = 0.109,

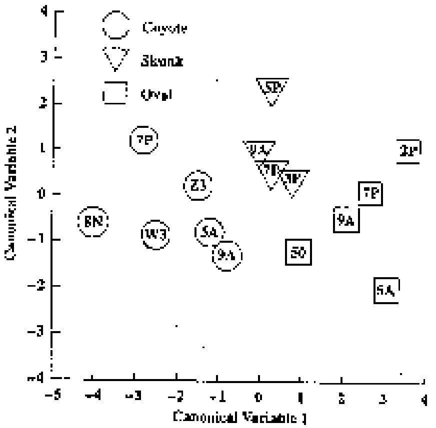

Fig. 2: Positions of the alarm calls elicited by the three silhouette models in discriminant space. The discriminant functions were calculated based on the means of the variables for all of the barks elicited from each animal during the first trial in which each animal produced an alarm call (Table 1). The labels within the symbols represent the dye marks placed on the pelage of each animal

F(8,18) = 4.558, p = 0.0036). The calls given in response to the coyote silhouette differed from both the skunk silhouette (F(4,9) = 3.691, p = 0.048) and the oval silhouette (F(4,9) = 10.971, p = 0.0016). The calls for the skunk and the oval did not differ significantly (F(4,9) = 2.951, p = 0.082). The stepwise procedure included four of the seven variables: the fundamental frequency, descending slope, dominant harmonic frequency and the interharmonic interval (Table 1). All of the calls were correctly classified into the expected silhouette-shape group based on the mean values of the call variables (Table 2).

All three silhouettes elicited similar numbers of alarm barks (Table 3; χ^2 (2, n = 15) = 0.02, p > 0.05) although different animals called to different silhouettes. Of the 10 prairie dogs that produced alarm calls in response to the silhouette presentations, only three called in response to more than one of the silhouettes; two of these called for all three silhouettes and a third called in response to two of the silhouettes (Table 3). The alarm barks produced by each of these animals were plotted in distinct regions of discriminant space for each of the silhouettes based on separate stepwise discriminant function analyses for each individual (Fig. 3). The discriminant functions calculated for the calls given by the two individuals that called to all three silhouettes (adult female 7P and adult male 9 A) included all of the original variables. All of the barks given by adult female 7P were correctly classified while 97% of the barks given by adult male 9 A were correctly classified (Table 4). The single discriminant function calculated for the barks given by the animal that called to two of the silhouettes (adult male 5 A) included the inter-

Table 1: $\bar{X}$ ± SE of the four alarm call variables that were included in the discriminant function analysis by the stepwise procedure

Variable	Stimulus coyote	 skunk	 oval
Fundamental Freq. (Hz) (±SE)	2419 ± 87	2303 ± 16	2264 ± 114
Descending Slope (Hz/ms) (±SE)	−48.2 ± 4.3	−57.7 ± 5.1	−39.5 ± 7.1
Dominant Harmonic (Hz) (±SE)	3870 ± 30	3627 ± 175	3853 ± 75
Inter-harmonic Interval (Hz) (±SE)	970 ± 90	2122 ± 14	801 ± 115

Table 2: Classification matrices calculated by a discriminant function analysis for calls elicited by three different shapes of silhouettes. The discriminant functions were based on mean call variables from 15 alarm calls recorded from 10 individual prairie dogs

Actual group	n	Predicted group membership coyote	 skunk	 oval
Coyote	6	6 (100%)	0	0
Skunk	4	0	4 (100%)	0
Oval	5	0	0	5 (100%)

Table 3: Numbers of alarm barks given by individual prairie dogs and mean numbers of alarm barks given in response to each of the three stimuli. All of the barks were emitted in single alarm calls with ≈0.1 s between successive barks. Although additional alarm calls were recorded, only the barks tabulated below were used to calculate the mean variables used in the discriminant function analysis

Individual	Sex	Stimulus coyote	 skunk	 oval
2P	F			22
3P	F		84	
5A	M	13		25
5O	F			39
5P	F		33	
7P	F	63	71	39
8N	M	30		
9A	M	54	33	63
W3	F	30		
Z3	F	91		
$\bar{X}$ (±SE)		47 (±12)	55 (±13)	38 (±7)

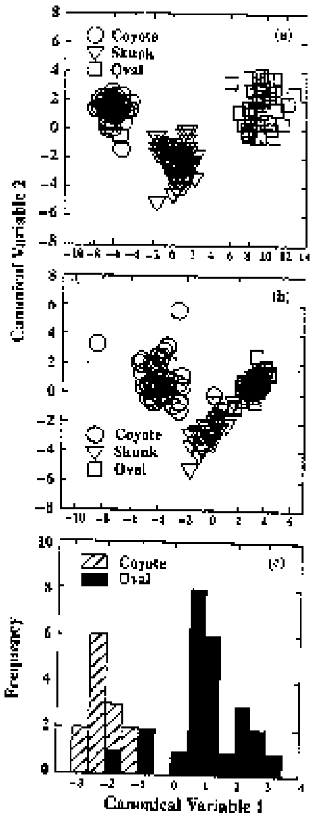

Fig. 3: Positions in discriminant space of the alarm barks elicited from the three prairie dogs that provided calls to more than one silhouette. Each discriminant function (Table 4) was calculated based on all of the alarm barks given by each animal during the first trial in which it called to each silhouette. (a) Adult female 7 P (b) adult male 9 A (c) adult male 5 A

harmonic interval, duration, supra-dominant harmonic frequency and the slope of the descending portion of the call. This discriminant function correctly classified 95% of the barks given by 5 A (Table 4).

The patterns of differences between the three treatments were similar among three of the four analyses. (The analysis of the barks given by 5 A include only one pairwise comparison as calls were only elicited by two of the silhouettes.) The greatest Mahalanobis' distances are between the calls given to the coyote and oval silhouettes; the Mahalanobis' distances between the coyote and skunk calls and the skunk and oval calls are less than half as large and are of similar magnitudes (Table 5).

Table 4: Percent correct classification for discriminant function analyses of alarm calls from individual prairie dogs. Separate discriminant functions were calculated for all of the barks from each individual

Individual	Stimulus coyote	skunk	oval
7 P[a]	63/63 (100%)	71/71 (100%)	39/39 (100%)
9 A[b]	51/54 (94.4%)	32/33 (97%)	63/63 (100%)
5 A[c]	13/13 (100%)		23/25 (92%)

[a] $CV_1 = (3.001)(DHF) + (0.309)(FF) + (1.995)(SHF) - (0.125)(DUR) + (0.143)(SLOPEA) + (0.187)(SLOPED) - (1.0)(IHI)$
$CV_2 = -(1.648)(DHF) + (0.076)(FF) + (1.959)(SHF) + (0.860)(DUR) - (0.430)(SLOPEA) + (0.266)(SLOPED) - (0.298)(IHI)$.

[b] $CV_1 = -(1.038)(DHF) - (0.007)(FF) + (0.726)(SHF) - (0.440)(DUR) - (0.554)(SLOPEA) - (0.069)(SLOPED) - (0.804)(IHI)$
$CV_2 = (11.427)(DHF) - (0.297)(FF) - (12.207)(SHF) - (0.392)(DUR) - (0.494)(SLOPEA) - (0.543)(SLOPED) + (2.403)(IHI)$.

[c] $CV_1 = -(0.383)(SHF) + (0.609)(DUR) - (0.268)(SLOPED) + (1.005)(IHI)$.

Table 5: Mahalanobis' distances (D^2) between all pairs of stimuli compared among the discriminant functions generated by the mean call variables and those generated by multiple barks from individual prairie dogs. Separate stepwise discriminant functions (Table 4) were calculated for the mean call variables for 15 alarm calls from 10 individuals (Means column) and all barks from an adult female (7 P) and two adult males (9 A and 5 A)

Pairwise comparison	$\bar{X}$	7 P	9 A	5 A
Coyote – skunk	9.84	55.71	24.69	
Coyote – oval	24.14	241.15	50.46	9.67
Skunk – oval	9.30	92.45	23.51	

The pooled within-groups correlations between the variables and the canonical discriminant functions for the analysis of the mean call variables show that the fundamental frequency had the greatest effect on the first discriminant function while the dominant harmonic frequency and the interharmonic interval had strong effects on the second discriminant function (Table 6). The analysis of all of the calls from adult female 7P showed that the interharmonic interval and the fundamental frequency were most highly correlated with the first discriminant function; the duration and slope of the ascending portion of the calls were most highly correlated with the second discriminant function. The interharmonic interval was again highly correlated with the first discriminant function in the analyses of the calls from the two adult males 9 A and 5 A. The slope of the descending portion of the calls was

Table 6: Pooled within-groups correlations between the discriminating variables and the canonical discriminant functions. The discriminating variables are listed in the order that they were entered by the stepwise procedure

Source of calls	Variables	Correlation with function 1	Correlation with function 2
Means	Fundamental freq.	0.361	0.126
	Descending slope	−0.166	0.054
	Dominant freq.	−0.053	−0.722
	Inter-harmonic	0.122	0.500
7P	Inter-harmonic'	−0.456	0.145
	Dominant freq.	0.148	0.208
	Duration	−0.004	0.851
	Ascending slope	−0.051	−0.371
	Fundamental freq.	0.318	−0.040
	Descending slope	0.131	0.195
	Supra-dominant freq.	0.015	0.227
9A	Inter-harmonic	0.744	−0.318
	Duration	−0.188	−0.330
	Ascending slope	0.285	0.314
	Descending slope	−0.239	0.414
	Supra-dominant freq.	0.137	−0.044
	Dominant freq.	0.042	0.059
	Fundamental freq.	−0.085	−0.169
5A	Inter-harmonic	0.826	
	Duration	0.301	
	Supra-dominant freq.	0.317	
	Descending slope	−0.402	

most highly correlated with the second discriminant function in the analysis of the calls from 9 A (Table 6).

The cluster analyses showed considerable individual variation in the calls within each treatment group (Fig. 4). The mean and the range of the squared Euclidean distances provide a measure for comparing the amount of individual variation among treatments. Within the calls to the coyote silhouette, the squared Euclidean distances had a mean of 1.138 and ranged from 0.064 to 3.575. The level of individual variation within the oval silhouette treatment was more consistent than within the coyote treatment; the range in the squared Euclidean distances was less than in the coyote treatment (0.228–2.514) but the mean distance was greater (1.224). There was much better agreement among the prairie dogs within the skunk silhouette treatment group (mean squared Euclidean distance = 0.527, range: 0.048–1.014). Considering the three animals that called to more than one silhouette, the two adult males (9 A and 5 A) consistently grouped far apart from the adult female (7P).

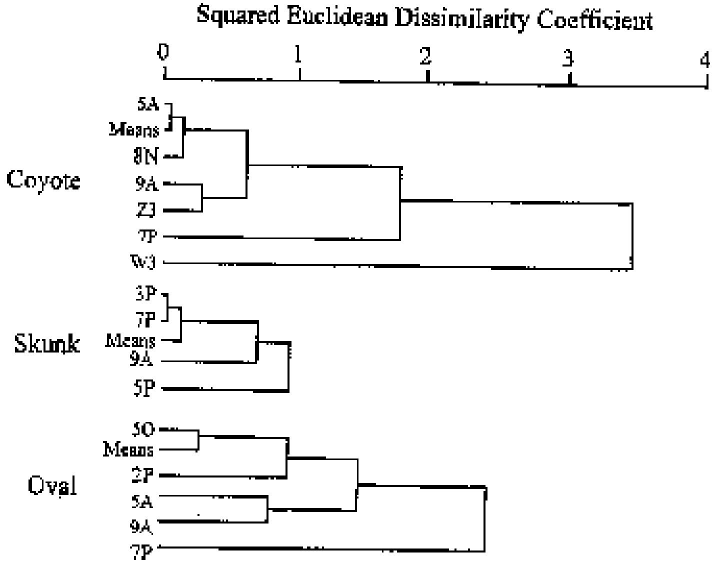

Fig. 4: Cluster analyses showing individual variation within each of the treatment groups. The squared euclidean distances were calculated based on the centroids of the four variables used in the discriminant function analysis of the mean variables (Table 1)

Discussion

Consistent differentiation among alarm calls given in response to three silhouette models differing in size and shape suggests that information about the size and shape of external stimuli is encoded in prairie dog alarm calls through variation in spectral characteristics of the calls. Although individual differences exist, the calls group together according to a common stimulus for discriminant functions based on mean call variables as well as for individual alarm calls (see Figs 2 and 3). This is consistent with the hypothesis that the first criterion of referential specificity, production specificity, is a characteristic of Gunnison's prairie dog alarm calls (see Evans et al. 1993).

Production specificity in the complete absence of behavioral variation among stimuli would indicate that prairie dogs form categories of their predators based on physical characteristics and not simply on the basis of response urgency as reported in other species of ground squirrels (e.g. Owings & Virginia 1978). Our reason for using silhouette models to elicit alarm calls was to control for behavioral variation among stimuli. Because the silhouettes differed in size, differences in apparent speed may have been perceived as behavioral variation by the prairie dogs. The pattern of movement interrupted by pauses and the lack of directional changes were identical among stimuli, however. Behavioral variation therefore was controlled to a great extent and the primary cues available to the prairie dogs were physical. Although behavioral variation among predators of a given species probably plays an important part in the production specificity of alarm calls in actual encounters with predators, our study shows that physical variation is important for production specificity in prairie dog alarm calls.

A question that emerges from the discriminant function results is: Which parameters of the alarm calls correspond to the ways that prairie dogs describe their predators? The pooled within-group correlations between the mean variables measured from the spectrograms and the canonical variables suggest that the fundamental harmonic frequency and a combination of the dominant harmonic frequency and the interharmonic interval are components of the descriptors of the size and shape of the eliciting stimuli (Table 6). However, the analyses of all of the calls from the prairie dogs that called to more than one silhouette show somewhat different patterns of variable loadings than the analysis of the mean call variables. These correlations are difficult to interpret because of unequal covariance matrices among the treatment groups. Although the covariance matrices were not significantly different in the analysis of the mean call variables (Box's M = 16.30, $p = 0.6373$), the covariance matrices from the analyses of all of the calls from adult female 7P and adult males 9 A and 5 A were unequal (7P calls: Box's M = 3672.6, $p < 0.0001$, 9 A calls: Box's M = 2787.8, $p < 0.0001$, 5 A calls: Box's M = 86.69, $p < 0.0001$). This is a result of the lack of independence among the calls given by these three prairie dogs during single trials. Pooling the covariance matrices is only valid if the observations are independent and the covariance matrices do not differ as in the analysis of the mean call variables (e.g. Dillon & Goldstein 1984; Bernstein 1988). The pooled within-group correlations for the analyses of all of the calls from 7 P, 9 A, and 5 A therefore should be interpreted with caution.

An important dimension of the variability in prairie dog alarm calls is individual variation within a stimulus category. There are several possible sources of individual variation including morphological differences in the larynx and oral cavity and behavioral differences related to experience with predators or motivation with regard to reproductive status. Morphological differences do not appear to be important here because different levels of individual variation are present among all three treatment groups (Fig. 4). If morphological differences are important, one would expect similar values of squared Euclidean distances within all three treatment groups.

Experience with predators is probably not important in this study because we used artificial stimuli to elicit the alarm calls. Although we intended two of the three silhouettes to represent familiar stimuli (i.e. the coyote silhouette as a predator and the skunk silhouette as a mammalian nonpredator) there is no reason to conclude that the prairie dogs recognized them. Alarm calls in response to live coyotes recorded during previous studies (e.g. Lewis-Wellman 1982; Kiriazis 1991) were significantly different from the alarm calls recorded during coyote silhouette presentations in this study (Wilks' lambda (4, 1, 10) = 0.049, F(4,7) = 33.88, $p < 0.001$). In addition, a live skunk that had been frequently observed scavenging for leftover trap bait never elicited alarm calls yet the skunk silhouette always caused a colony-wide response similar to that observed during encounters with predators. Although the type of call and the behaviors associated with calling during the silhouette presentations were identical to those observed during encounters with predators, the coyote and skunk silhouettes may have been just as novel to the prairie dogs as the oval silhouette. The differences among the alarm calls in response to the silhouettes can therefore be attributed to differences in the physical characteristics of the stimuli rather than response urgency based on past experience with coyotes or skunks.

An additional consideration with respect to individual variation is that prairie dogs of different sex and/or age classes may have different motivation for calling. Adults with young would be expected to provide reliable information to maximize the chance of their offspring responding with the most effective escape strategy (e.g. Sherman 1977). Non-reproductive adults, particularly those on the periphery of the colony, may call manipulatively to increase the level of colony-wide vigilance to enhance their own safety (e.g. Dawkins & Krebs 1978). Finally, less experienced individuals may not have sufficient experience adequately to encode all of the information associated with a given predator category.

Our study shows that Gunnison's prairie dogs may encode information in their alarm calls about the physical characteristics of external stimuli. Despite controlling for most aspects of the behavior of the eliciting stimuli constant, prairie dog alarm calls varied consistently primarily with physical characteristics of the stimuli. This provides the potential to encode the information necessary to identify different classes of predators. If further studies reveal that behavioral variation among predators of a particular species can generate production specificity as well, then receivers could adjust their responses for behavioral variation among individuals within a predator class.

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Reproductive Decisions in Female European Ground Squirrels: Factors Affecting Reproductive Output and Maternal Investment

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Abstract

Physiological and behavioural parameters associated with reproductive effort and success were investigated in female European ground squirrels *Spermophilus citellus*. The proportion of reproductive (lactating) females in the study population was over 90% and was not related to age. Timing of oestrus and ovulation was found to be affected by the female's emergence date and condition. Females with low emergence mass showed delayed oestrus. Differences in ovulation dates were shown to affect reproductive output in terms of litter size and sex ratio. Early litters were larger and male biased. X-ray techniques were used to determine intrauterine litter size in individual females. The results indicated that litter size and sex ratio were fixed prenatally. Lactation costs were reflected in the intensity of mass loss and duration of lactation. Mass loss varied with litter size, in that females with large litters showed a more rapid loss than others. The second parental investment parameter, lactation duration, varied among individual females and was dependent on the timing of reproduction and litter size (except yearlings). Early born litters, which were, in most cases, larger than later ones, were nursed longer. Prolonged lactation periods affected female condition in that they started prehibernation fattening later and entered hibernation with a lower mass than individuals that had shorter lactation periods. Yearling females probably could not afford the energetic costs of long lactation, independent of their offspring number. These results indicated that females with higher reproductive output and higher investment were unable to compensate these costs before hibernation. Consequences for these individuals could therefore be lower over-winter survival or a delayed oestrus in the following season.

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Introduction

In hibernating mammals such as the European ground squirrel *Spermophilus citellus*, reproduction is often affected by the accompanying temporal and energetic constraints. Females have to complete mating, gestation, lactation and pre-hibernatory fattening during a short active season. Juveniles also have to grow and prepare for hibernation. Hence, as in *S. citellus*, females can only produce one litter per year. In addition to the limited time budget, habitat quality declines with seasonal progression. As a result, late-born juveniles have both less time to gain fat stores and lower food quality. In line with these factors, it has been shown in

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