Alarm signals of the great gerbil: Acoustic variation by predator context, sex, age, individual, and family group

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The great gerbil, *Rhombomys opimus*, is a highly social rodent that usually lives in family groups consisting of related females, their offspring, and an adult male. The gerbils emit alarm vocalizations in the presence of diverse predators with different hunting tactics. Alarm calls were recorded in response to three predators, a monitor lizard, hunting dog, and human, to determine whether the most common call type, the rhythmic call, is functionally referential with regard to type of predator. Results show variation in the alarm calls of both adults and subadults with the type of predator. Discriminant function analysis classified an average of 70% of calls to predator type. Call variation, however, was not limited to the predator context, because signal structure also differed by sex, age, individual callers, and family groups. These variations illustrate the flexibility of the rhythmic alarm call of the great gerbil and how it might have multiple functions and communicate in multiple contexts. Three alarm calls, variation in the rhythmic call, and vibrational signals generated from foot-drumming provide the gerbils with a varied and multi-channel acoustic repertoire. © *2005 Acoustical Society of America.* [DOI: 10.1121/1.2031973]

I. INTRODUCTION

Alarm vocalizations can contain multiple messages. Ground-dwelling rodents and primates call to warn group members of danger (Sherman, 1977; Seyfarth *et al.*, 1980; Hoogland, 1996; Blumstein and Armitage, 1997). The alarm signals convey referential information about the specific type or category of predator (Seyfarth *et al.*, 1980; Zuberbühler, 2000, 2001), degree of risk as often determined by distance from the predator (Owings and Hennessy, 1984; Burke da Silva *et al.*, 1994; Blumstein, 1995; Randall and Rogovin, 2002), size and shape of the predator (Evans *et al.*, 1993; Ackers and Slobodchikoff, 1999), and amount of arousal (Hammerschmidt and Fischer, 1998) or emotional state (Evans, 1997). Alarm signals also act in the self-interests of the caller by reducing its vulnerability. The calls assemble conspecifics to attack the predator as a group (Seyfarth *et al.*, 1980) or cause conspecifics to scatter and confuse the predator (Sherman, 1985). The target of an alarm may also be the predator in which the alarm communicates detection and alertness to deter pursuit (Caro, 1995; Randall and Matocq,

1997). The signals are not mutually exclusive, however, and multiple messages can be transmitted in alarm calls (Zuberbühler *et al.*, 1997), including information about the identity of the caller (Cheney and Seyfarth, 1988; Hare, 1998; Hare and Atkins, 2001; McCowan and Hooper, 2002; Blumstein and Munos, 2005).

The great gerbil, *Rhombomys opimus*, is unique among murid rodents in the subfamily Gerbillinae because it is the only species known to give alarm vocalizations in conjunction with footdrumming in the presence of predators (Randall *et al.*, 2000). Great gerbils live in family groups consisting of a male with one to six females and their offspring (Kutcheruk *et al.*, 1972; Naumov and Lobachev, 1975; Randall *et al.*, 2000). Females are philopatric and highly related; males disperse into family groups and are usually unrelated to the females (Randall *et al.*, 200■). All family members footdrum and give vocal and visual displays in the presence of diverse predators: monitor lizards, snakes, dogs, foxes, weasels, polecats, and humans (Nikolsky, 1970, 1984; Randall *et al.*, 2000; Randall and Rogovin, 2002). As a predator or threat approaches, the gerbils stand in a bipedal posture

and give a rhythmic call consisting of repetitive chevron-shaped notes at intervals of 0.2–0.5 s. If the threat continues, the gerbils emit a call (intense) with notes as couplets and an internote interval averaging 0.07 s. Gerbils also give a short whistle and immediately run into the burrow when startled by the sudden arrival or the fast movement of a terrestrial predator and in response to aerial predators. [See Randall and Rogovin (2002) for spectographs of all three alarm calls.] In general, about 70%–80% of alarm calls are rhythmic, 10%–20% intense, and 10%–20% whistles. Playback tests revealed that great gerbils can distinguish the three calls and respond differently to them (Randall and Rogovin, 2002). Although the gerbils stopped feeding and stood in an alert posture to all three calls, they were more vigilant in response to the intense call and the whistle than to the rhythmic call. The calls apparently function to communication degree of risk or "response urgency" (Blumstein and Armitage, 1997).

The question of whether gerbils might classify alarm vocalizations by their meaning and use them to identify the category of predator in "functionally referential" calls was not addressed by Randall and Rogovin (2002). The strongest evidence for semantic alarm systems in mammals comes from studies of primates (Cheney and Seyfarth, 1988; Pereira and Macedonia, 1991; Fischer, 1998; Zuberbühler, 2000, 2001), whereas studies of rodents show that their alarm calls usually function to communicate risk or "response urgency" (Leger *et al.*, 1979; Blumstein, 1995; Blumstein and Armitage, 1997). However, predator-specific alarm calls have been documented in rodents as well (Greene and Meagher, 1998). We wondered, therefore, whether great gerbils produce sufficient variation in their alarm calls to communicate more than the degree of risk (Hare, 1998; Hare and Atkins, 2001; Blumstein and Munos, 2005; Blumstein *et al.*, 2004). With this question in mind we conducted a detailed analysis of the most common alarm call of the gerbils, the rhythmic call, for differences in call structure that could function to provide potential information about the caller as well as about the type and hunting style of the various predators. We tested whether (1) signals differ according to the type of predator in subadults and adults and predicted more variation in subadults (Randall, 1995; Blumstein and Daniel, 2004); (2) males and females emit structurally different calls; (3) calls vary by age category; (4) members of family groups emit calls unique to the group; and (5) calls of individual gerbils are distinctive.

II. METHODS

A. Subjects, study site, and observation

We studied the great gerbil on the Ecocentre Dzeiran, a reserve for endangered Asian gazelles, in the Kyzylkum desert of Uzbekistan about 30 km south of Bukhara (39°35′–39°40′N 64°36′–64°43′E). We recorded alarm calls in 1999 and 2000. The 1999 population had a very high density (94% of burrow systems were occupied with a mean group size of 13.0+1.8 animals, $n=41$ groups) because of favorable conditions for reproduction in 1998 and spring 1999. Very dry conditions beginning in late spring of 1999 caused high mortality so that population density in 2000 was

much lower (40% of burrow systems were occupied with group size equal to 7.6±1.3 individuals) and there was a significant turnover in the population. This fluctuation in density reflects patterns typical for desert environments.

We identified and numbered family groups and captured and marked individuals in the spring and fall. We distinguished different-aged gerbils by weight and stage of reproduction in each family group. Adults were fully grown, reproducing animals (130–200 g); subadults were young gerbils born in that year that almost approached adult size (about 90–120 g). Pups were small animals, recently emerged from the burrow, that weighed 30–90 g.

We captured individual gerbils with $30 \times 15 \times 15$ cm³ wire-mesh live-traps baited with a mixture of rolled oats, sunflower seeds, carrots, greens, and peanut butter. We marked each animal with numbered ear tags (Monel #1) and clipped brown guard hairs on the backs and sides of adults to expose unique patterns in the underhairs for individual identification at a distance. All pups from the same litter had the same mark. We monitored females for signs of pregnancy and lactation so we could predict the emergence of pups. Pregnancy was determined by weight gain and lactation by the appearance of swollen, pink nipples. We observed gerbils with binoculars at a distance of 20–40 m and recorded behavior by speaking quietly into a hand-held tape recorder. The gerbils habituated to a human sitting quietly on the ground behind low vegetation.

B. Vocal recording

1. Human approaches

We recorded alarm calls in the field from 23 March to 12 June 1999, with a Sennheiser (Md 421 U4) microphone through a 25-dB preamplifier into a Marantz stereo cassette recorder (PMD 201). We also recorded vocalizations from 5 April to 22 May and 23 October to 6 November 2000 with the same microphone arrangement but with a DAT Sony 8 recorder (TCD-D8).

Calls were recorded in response to human approaches by walking slowly toward a family group until gerbils began to give alarm calls or escaped into the burrow. The human continued walking toward the calling gerbil or center of the group if gerbils were in the burrow. At approximately 10–15 m the human stood and recorded calls of the calling gerbil or waited for gerbils to emerge and give alarm calls. When a gerbil emerged and stood in bipedal posture the microphone was pointed toward it. If no call was given, the human moved a few steps toward the gerbil, which caused the gerbil either to call or run into a burrow.

We recorded calling bouts (a continuous series of calls) from individually identified adults and pups and subadults, which were not individually marked but had a group-specific mark. In spring 1999 we recorded 95 calling bouts from gerbils in 21 different family groups. In spring 2000, we recorded 39 calling bouts of animals in 8 family groups. In the fall, we recorded 65 calling bouts in 19 family groups to yield a data set of 9712 calls for the 2 years. After elimination of unidentified animals and whistles and intense calls we had a data set of 6309 rhythmic calls of adults, subadults,

TABLE I. Summary acoustic variables used in analyses.

Acoustic variable	Description
Minimum frequency	Lowest frequency attained by call in Hz
Maximum frequency	Highest frequency attained by call in Hz
Mean frequency	Average frequency across call in Hz
Frequency range	Peak frequency minus minimum frequency in Hz
Maximum frequency/mean frequency	Peak frequency divided by mean frequency
Mean frequency/minimum frequency	Mean frequency divided by minimum frequency
Frequency peak amplitude	Frequency at which peak amplitude occurs in Hz
Minimum frequency location	Location minimum frequency in call as % duration
Maximum frequency location	Location peak frequency in call as % of duration
Duration	Length of call measured in ms
Start slope	Slope of initial third of call contour in Hz/ms
Middle slope	Slope of middle third of call contour in Hz/ms
Final slope	Slope of final third of call contour in Hz/ms

and pups of which 3630 were from adults (2000 calls from females and 1630 males) with the remainder from subadults and pups.

2. Different predator contexts

To answer the question of whether great gerbil alarm calls have productional specificity, we recorded alarm calls of adults and subadults in the presence of three different predators with different hunting tactics. We recoded alarm calls to a known predator, the gray monitor lizard, *Varanus griseus* (Cellarius *et al.*, 1991; Rogovin *et al.*, 2004), and a representative of a live mammalian predator, a wolfhound hunting dog, *Canis familiaris*. The lizard hunts by entering larger burrows and digging into smaller ones whereas a canid would run and pounce and not be able to enter the burrow. A human (K. Collins) represented the third predator category.

We tethered a large monitor lizard (1.4-m snout-vent length) in the center of the active area of 16 family groups. The tether was made of a braided cotton rope that was tied like a belt just anterior to the lizard's hind legs. A 2-m length of nylon robe, tied to the belt, was attached to a stake inserted into the ground. The lizard could move and dig within a 2-m radius. The dog was also tethered in the center of family groups ($n=17$) with a 2-m cotton rope tied to a stake inserted in the ground. The dog could also move on the tether. The activity of tethering the predator caused the gerbils to run into the burrow. While the gerbils were in their burrows, the person recording the alarm calls hid from view behind vegetation about 20 m away and recorded calls with the Sennheiser microphone through a 25-dB preamplifier into the Marantz stereo cassette recorder as gerbils emerged and began to emit alarm vocalizations. Identification of the caller and the time called was recorded separately into a hand-held Sony M530 micro-cassette recorder. Because we recorded free-ranging animals, we could not control the distance between the predator and caller and estimate that the distance ranged from about 5 to 20 m.

All calls to humans used in the analysis were recorded at an approximate distance of 5 to 20 m from the gerbil during spring 1999 in the same family groups in which the lizard and dog were tethered. Although we recorded calls in the same family groups, we only used a calling bout from an individual once in the same data set. Because of high densities and the large number of gerbils in family groups we sometimes were unable to identify the caller. After elimination of recordings of unknown callers and pups we had 1415 alarm calls of 17 individually marked adults and 628 calls from 13 subadults from 13 different families.

C. Acoustic analysis

Vocal recordings were digitized onto a Micron Pentium Computer using a SoundBlaster soundcard (sampling rate up to 44.1 kHz) and Cool Edit Pro Signal Analysis software (sampling rate of 44.1 kHz and using 512-point FFT with a Hamming filter for generating spectrograms). Acoustic files were filtered for background noise using standard parametric filtering in Cool Edit Pro on the PC computer, and each call was cued for subsequent digital analysis.

D. Statistics

We measured acoustic variables in 3630 rhythmic alarm calls recorded from 46 individual adults using a modified version of the technique described in McCowan (1995) and McCowan and Reiss (2001). [See Randall and Rogovin (2002) for spectogram of call.] The computer measured 60 points of frequency, amplitude, and time across the duration of each call using a 1024-point FFT with a Hamming filter from the spectrum taken at each time point. After call digitization and measurement were completed, we conducted subsequent calculations to obtain summary acoustic variables that defined spectral, temporal, amplitude, and contour variables of the calls. (See Table I for a list of analyzed variables.)

The outcomes and covariates of the statistical tests were either categorical or continuous in structure. Thus, mixed effects linear models (Pinheiro and Bates, 2000) (with individual as the grouped random effect for repeated measure) and discriminant function analysis (DFA) were the statistical methods of choice. Continuous variables were tested for and confirmed for normality. Covariates included individual, sex, age, and context (lizard, human, or dog induced).

All statistical tests were conducted using programmable S-Plus statistical software. The linear mixed effects model

TABLE II. Results of analysis of 13 acoustic variables for the gerbil rhythmic alarm call by sex (df=1,3440), age (df=2,6199) and predator context for subadults (df=2,697) and adults (df=2,1394) using the F-statistic from the linear mixed effects model (LME) in S-Plus with ID as the grouped random effect variable (Pinheiro and Bates, 2000). Pairwise tests denoted by superscripts for significant variables with more than two categories are also presented [age: P=pup, S=subadult, A=adult; predator context for subadults and adults: D=dog, H=human, L=lizard; includes differences between adults (listed first) and subadults when they occurred].

| | | | Context | | |
Acoustic variables	Sex	Age	Subadults	Adults	Pairwise tests
Minimum frequency	348.1[d]	333.12[d]	102.38[d]	229.26[d]	P[a],S[a],A[b]; D[a],H[b],L[c]
Maximum frequency	1.86	9.08[c]	212.61[d]	36.13[d]	P[b],S[a],A[b]; D[a],H[b],L[c]
Mean frequency	3332.05[d]	386.11[d]	162.62[d]	116.22[d]	P[a],S[b],A[c]; D[a],H[b],L[c]
Frequency range	3.21	19.62[d]	135.39[d]	48.58[d]	P[a],S[a],A[b]; D[a],H[b],L[c]
Maximum frequency/ mean frequency	4.74[a]	35.61[d]	97.16[d]	19.25[d]	P[a],S[a],A[b]; D[a],H[b],L[c]
Mean frequency/ minimum frequency	0.49	1.17	2.46	1.51	
Frequency at peak amplitude	321.83[d]	321.74[d]	159.13[d]	64.45[d]	P[a],S[b],A[c]; D[a],H[b],L[c]; D[a],H[a],L[b]
Minimum frequency location	143.92[d]	52.85[d]	15.84[d]	2.60	P[ab],S[a],A[b]; D[a],H[b],L[b]
Maximum frequency location	99.05[d]	37.71[d]	8.67[c]	2.37	P[a],S[a],A[b]; D[a],H[a],L[b]
Duration	2.38	0.79	164.16[d]	0.52	L[a],H[b],D[b]
Start slope	32.86[d]	18.03[d]	15.17[d]	14.21[d]	P[a],S[a],A[b]; D[a],H[b],L[a]; D[a],H[a],L[b]
Middle slope	15.29[c]	36.24[d]	61.58[d]	8.34[c]	P[a],S[a],A[b]; D[a],H[b],L[c]; D[a],H[ab],L[b]
Finish slope	26.57[d]	30.86[d]	41.10[d]	0.57	P[a],S[a],A[b]; D[a],H[b],L[c]

[a]p<0.05.
[b]p<0.01.
[c]p<0.001.
[d]p<0.0001.

included individual as a grouped random effect variable. Therefore all *p* values were appropriately adjusted to variance imposed by this repeated measure, which also corrected for pseudoreplication. We checked for variance problems by plotting residuals versus fitted values and used a within-group variance structure, usually the "exponential" function, to correct variance problems (S-Plus outputs confidence intervals for variance structure and random effects.). We also tested for problems using within group correlation with S-Plus, but did not find any. We used S-Plus to conduct Bonferroni corrected, pairwise tests on each model generated using the following command: anova(<model name,L=c (<factor name1=1, <factor name 2=−1) .

All 13 summary variables as described in Table I were entered into the DFA. Cross validation in the DFA was done with the "leave-one-out" method. We conducted two sets of DFA. In one set we used all samples of rhythmic calls available for each classification by age, sex, context, individual identity, and family group. We then conducted a second series of DFA with much smaller, but balanced, sample sizes (randomly selected from the original data set) to verify that our unbalanced data were not biased. Because of questions about the use of unbalanced designs in DFA we report both sets of data.

The calls of adults and subadults in response to the three predator stimuli were analyzed separately after we determined that the calls varied by age. We were unable to separate by sex because of small sample sizes and unknown sexes of subadults. We also used mixed-sex groups for comparisons in the age category of adults, subadults, and pups. We selected to analyze for individual differences in animals from 1999 and 2000. The animals recorded in 1999 had been on the study site for at least a year in stable family groups. In 2000 there was a large turnover in animals and dispersal in the fall so that the family groups were not considered as stable. We were therefore interested to see whether calls were less consistent in 2000 compared with 1999. All calls analyzed for differences by age, sex, individual, and family group were responses only to humans.

III. RESULTS

A. Differences in predator-induced calls

Gerbils showed significant acoustic differences in rhythmic call structure in the predator context. Eight of 13 acoustic variables for adults and 12 of 13 variables for subadults differed significantly (Table II). Paired tests demonstrated further that acoustic variables differed in the three predator contexts. For adults, we found significant differences between calls to the dog and human in 10 of 13 variables and to the lizard-human and lizard-dog calls in 11 of 13 variables. For subadults, the comparison between dog and human was significant in only 7 of 13 variables, but the dog and lizard comparison differed by 12 of 13 acoustic variables and the human-lizard comparison in 10 of 13 acoustic variables (Tables II and III).

Cross-validation DFA using pooled data from individuals on the 13 acoustic variables revealed a high classification by type of predator for adults (65%–73%) and subadults (64%–96%) and general agreement in classifications in the balanced and unbalanced designs (Table IV).

TABLE III. Mean±SE of 13 acoustic variables measured in three different predator contexts for adults. See Table II for results from paired comparisons.

Acoustic variable	Dog		Human		Lizard	
	Adult	Subadult	Adult	Subadult	Adult	Subadult
Minimum frequency	1764.6±32.0	2005.3±20.4	1707.4±10.1	2233.7±16.7	1239.1±18.9	1829±16.3
Maximum frequency	2413.9±25.4	2585.0±17.0	2077.2±13.5	2386±14.3	2278.6±12.9	2171.1±11.5
Mean frequency	2207.3±21.9	2380.6±13.0	1970±11.68	2341.2±14.8	1945.3±11.6	2085.5±11.1
Frequency range	649.2±36.6	579.7±22.10	369.8±11.7	153.2±7.5	1039.4±16.0	341.7±14.6
Maximum frequency/ mean frequency	1.098±0.01	1.087±0.0045	1.052±0.002	1.099±0.001	1.18±0.009	1.042±0.002
Mean frequency/ minimum frequency	2.46±0.59	2.156±0.56	1.052±0.002	1.050±0.004	1.661±0.026	1.202±0.054
Frequency at peak amplitude	2312.96±36.6	2475.14±14.5	2052.00±12.9	2365.40±14.7	2119.6±16.3	2155.35±10.6
Minimum frequency location	0.635±0.033	0.379±0.028	0.29±0.14	0.175±0.028	0.36±0.027	0.216±0.025
Maximum frequency location	0.54±0.017	0.59±0.013	0.60±0.005	0.62±0.013	0.62±0.012	0.54±0.01
Duration	54.17±2.36	50.90±0.656	55.93±4.93	35.21±0.63	61.19±4.77	53.44±0.77
Start slope	1.72±0.217	1.20±0.13	1.44±0.05	0.80±0.068	3.73±0.154	1.60±0.09
Middle slope	0.35±0.24	0.46±0.028	0.24±0.014	0.30±0.019	0.423±0.073	0.11±0.015
Finish slope	−2.16±0.298	−1.76±0.028	−1.21±0.47	−0.39±0.05	−3.21±0.144	−1.14±0.07

B. Differences by sex

We found a significant difference in the acoustic structure of adult males and females in 8 of 13 acoustic variables (Tables II and V). Females had a greater minimum and mean frequency and a lower frequency range than males. Variables of minimum and maximum frequency location and start, middle, and final slope also differed significantly (Table V). DFA using pooled data from individuals on these variables revealed that 65% (balanced design) to 70% (unbalanced design) of calls were correctly classified to the appropriate sex class (Table IV).

C. Differences by age

Eleven of 13 acoustic variables differed by age category (Tables II and V). Although sex might account for some of the variation in our analysis, we found clear differences between the calls of adults and younger gerbils. Adults differed significantly from subadults on 11 of 13 variables and from pups on 9 of 13 variables (Table II). Pups and subadults only differed significantly on 3 of 13 acoustic variables: minimum frequency, mean frequency, and frequency at peak amplitude. In almost every comparison the calls of pups and subadults had higher frequencies than adults (Tables III and V).

DFA using pooled data classified 45% (balanced design) to 50.4% (unbalanced design) of the calls correctly by age group (Table IV). Of these, subadults and pup calls were the most varied and showed a lower classification than adults.

D. Individual differences

We found evidence for individual differences in the rhythmic alarm call. Cross-validation DFA revealed that individuals could be distinguished based upon the acoustic structure of their rhythmic calls (Table IV). Average percent correct classification across 8 individuals in 1999 was 75.4% (range for individuals, 37%–100%) and 40% for 16 individuals in 2000 (range=13%–74.6%). When we reanalyzed the data using a balanced design we found even higher rates of classification. Average percent classification across 6 individuals in 1999 was 82% (range=71%–97%) and across 18 individuals in 2000 was 65% (range=20%–100%). Because percent correct classification (PCC) by chance alone was only 6%, this average percent correct classification represents significant discrimination for individual calls.

E. Family group differences

DFA using pooled data from individuals on the 13 acoustic variables revealed that 60%–89% of calls were correctly classified to the appropriate family group in the spring and 38%–70% in the fall of 2000 in the balanced design (Table IV). Classification in the unbalanced design was similar to the balanced design for the fall (39%–71%) and somewhat lower for the spring (50%–76%).

IV. DISCUSSION

Could the alarm calls of the great gerbil contain specific information about type and hunting tactics of predators as well as general information about predation risk? Alarm calls that communicate both risk and referential information about predators do occur (Zuberbühler, 2000; Manser, 2001; Fichtel and Kappeler, 2002). Our analysis revealed that gerbils varied the rhythmic alarm call with the type of predator. It seems possible, therefore, that the level of response urgency is reflected in changes in acoustic structure of the call as well as in call rate and duration when gerbils switch from the rhythmic alarm to the intense alarm or the whistle (Manser, 2001). Since the rhythmic call is usually given when a predator is some distance away and the situation is not life-threatening, gerbils have time to communicate information about predator type in the rhythmic call before communicating response urgency in the intense call or whistle when the situation becomes more threatening.

TABLE IV. Results from cross validation tables of discriminant function analyses showing percentage of calls correctly classified by sex, age, predator context, individual, and family group in both balanced (Bal) and unbalanced (Unbal) designs. Included are the number of calls analyzed, number of animals giving the calls, and sex ratio in groups.

Category	Percent Classified		No. of calls		No. of animals		Group composition	
	Bal	Unbal	Bal	Unbal	Bal	Unbal	Bal	Unbal
Sex								
Male	67	72	1127	1630	14	14	All adult	All adult
Female	63	69	1127	2000	32	32	All adult	All adult
Age								
Pup	36	54	1331	1348	14	14	Unknown sex	Unknown sex
Subadult	40	36	1331	1331	14	19	Unknown sex	Unknown sex
Adult	58	61	1331	3576	14	45	10F, 4M	31F, 14M
Predator context								
Adult								
Dog	73	72	60	196	4	4	3F, 1M	3F, 1M
Human	70	73	60	950	4	12	4F	9F, 3M
Lizard	68	65	60	269	4	4	2F, 2 sex unknown	2F, 2 sex unknown
Subadult								
Dog	76	64	45	208	3	5	All unknown sex	
Human	96	92	45	175	3	5	All unknown sex	
Lizard	80	91	45	245	3	3	All unknown sex	
Individuals (all adults)								
1999	82	75	210	862	6	8	4F, 2M	5F, 3M
2000	64	40	450	2082	18	16	13F, 5M	13F, 3M
Family Groups (all adults)								
Spring 2000								
A	89	76	45	270	3	3	2F, 1M	2F, 1M
B	89	79	45	162	3	4	3F	3F, 1M
C	60	50	30	66	2	2	1F, 1M	1F, 1M
Fall 2000								
A	38	39	60	463	2	5	2F	4F, 1M
B	57	58	60	116	2	2	1F, 1M	1F, 1M
C	70	71	60	300	2	2	2F	2F
D	57	50	60	89	2	2	2F	2F

Functionally referential alarm calls must show a strong association between a specific event or object and a particular call and elicit a unique behavioral response (Evans, 1997). They are most likely to evolve when animals are hunted by predators with different hunting strategies which require different modes of escape (Macedonia and Evans, 1993). The great gerbil is preyed on by a variety of terrestrial and aerial predators that employ different hunting tactics. Major terrestrial predators that enter burrows include the marbled polecat (*Vormela perigusna*) (Bekenov, 1982), a fast moving predator especially adapted for hunting rodents in burrows, the monitor lizard, and various snake species. Mammalian predators unable to enter the burrow that depend on stealth include steppe cats (*Felis libicus*) and foxes (*Vulpes vulpes, Vulpes corsac*). Survival depends on different escape responses to these varied predators. For instance, instead of running into the burrow, gerbils exit the burrow when a predator goes inside. An entire family group may move into a new burrow system in response to the arrival of a polecat in the colony ($n=11$, unpublished observations).

Variation in the rhythmic alarm call was not limited to predator context in the gerbils, and the calls differed among individual callers and family groups as well as by sex and age. Because great gerbils have no long-distance vocalizations other than alarm signals, evolution of a secondary function in the calls to convey information in the social group would be adaptive. Individual differences in alarm calls have already been documented in other social rodents (Owings and Leger, 1980; McCowan and Hooper, 2002; Blumstein and Munos, 2005), and animal signals often have more than one function and occur in different contexts (Smith, 1991; Tamura, 1995; Reby *et al.*, 1999). It, therefore, seems reasonable that alarm signals could also be signals of identity in highly social mammals.

Why would individual identity be conveyed in alarm calls? One hypothesis is that individually distinctive alarm calls evolve so that the receiver can evaluate reliability of the caller (Krebs and Dawkins, 1984; Hare, 1998; Blumstein *et al.*, 2004). Response to unreliable or false alarms may cause an animal to waste time and energy (Cheney and Seyfarth,

TABLE V. Mean±SE of 13 acoustic variables measured for differences by sex and age. See Table II for paired comparisons by age.

Acoustic variable	Sex		Age		
	Male	Female	Adult	Subadult	Pup
Minimum frequency	1631.65±6.84	1987.70±7.32[a]	1729.5±5.2	1853.88±7.9	1985.26±9.85
Maximum frequency	2574.02±49.1	2680.51±35.39	2673.14±30.33	2515.36±9.69	2753.61±31.19
Mean frequency	2034.87±8.18	2222.89±7.01[a]	2142.90±5.59	2285.66±7.61	2419.28±10.07
Frequency range	942.37±50.02	872.80±35.59[a]	943.64±30.23	661.48±10.87	768.35±30.23
Maximum frequency/ mean frequency	1.22±0.02	1.18±0.01	1.22±0.010	1.10±0.003	1.12±0.007
Mean frequency/ minimum frequency	1.51±0.17	1.40±0.07	1.41±0.08	1.32±0.05	1.23±0.005
Frequency at peak amplitude	2080.77±8.94	2279.26±7.31	2192.0±5.92	2335.31±7.60	2462.61±10.80
Minimum frequency location	0.28±0.01	0.45±0.01[a]	0.36±0.007	0.51±0.01	0.43±0.012
Maximum frequency location	0.60±0.005	0.53±0.005[a]	0.56±0.003	0.52±0.006	0.50±0.006
Duration	371.2±203.2	98.78±76.0	223.65±92.2	89.59±0.76	89.71±0.71
Start slope	1.18±0.03	0.80±0.06[a]	0.91±0.3	1.195±0.03	1.17±0.05
Middle slope	0.013±0.006	0.059±0.02[a]	0.086±0.01	−0.089±0.01	−0.13±0.045
Finish slope	−0.098±0.14	−0.79±0.14[a]	−0.37±0.08	−1.26±0.04	−0.94±0.07

[a]All $P < 0.01$.

1985, 1988; Bachman, 1993), lose resources (Munn, 1986; Møller, 1988), and mating opportunities (Møller, 1990). Recent studies of Richardson ground squirrels (Hare, 1998; Hare and Atkins, 2001) and yellow-bellied marmots (Blumstein *et al.*, 2004) demonstrated that individual distinctiveness in alarm calls is related to estimates of reliable signals by the receiver. Whether great gerbils have the same ability should be tested in future experiments.

The discovery that alarm calls are distinctive to family groups is an interesting result. In general, group-distinctive calls have been demonstrated in few mammals (Boughman, 1997), although birds use calls to recognize group membership (Hopp *et al.*, 2001). Family groups in the spring had a somewhat higher correct classification of alarm calls than family groups in the fall when dispersal was occurring. Because great gerbils are very territorial, recognition of neighbor calls may be an important spacing mechanism (Frommolt *et al.*, 2003).

Age differences occur in the structural characteristics of rodent alarm calls (Nesterova, 1996; Blumstein and Daniel, 2004; Blumstein and Munos, 2005). We found that the rhythmic alarm call of adult gerbils differed from the calls of subadults and pups on 85% and 69% of acoustic variables, respectively, compared with the calls of pups and subadults differing on only 23% of the acoustic variables. Subadult and pups had lower classification in the DFA than adults. These results suggest that some learning and refining of call structure may occur in the younger animals. In contrast, although we predicted that subadults might demonstrate less consistency in their calls than adults because of less experience, we found that the rhythmic call of subadults had an even higher classification by predator type than adults. If there is a learning period for production of predator-specific calls, it must occur before gerbils are reproductive adults.

The variations in the rhythmic alarm call of the great gerbil illustrate the flexibility of alarm signals and how they might have multiple functions and communicate in multiple contexts (Partan and Marler, 1999). Calls that serve different functions can be acoustically quite similar, and listeners can learn to discriminate between the different call types (Fischer *et al.* 2001, 2002). The variation in the rhythmic alarm call, the two other call types (intense and whistle), and vibrational signals generated from footdrumming provide great gerbils with a varied and multi-channel acoustic repertoire (Randall *et al.*, 2000; Randall and Rogovin, 2002). How much of this acoustic variation is meaningful and can be discriminated by the great gerbil to make adaptive responses must be investigated in future studies to understand fully their communication system and how it compares with other social mammals.

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