ANIMAL BEHAVIOUR, 2008, **76**, 1055–1064
doi:10.1016/j.anbehav.2008.06.002

Available online at www.sciencedirect.com
ScienceDirect

The structure, meaning and function of yellow-bellied marmot pup screams

DANIEL T. BLUMSTEIN*†, DOMINIQUE T. RICHARDSON*, LOUISE COOLEY†, JAMIE WINTERNITZ*† & JANICE C. DANIEL*†
*Department of Ecology and Evolutionary Biology, University of California, Los Angeles
†Rocky Mountain Biological Laboratory, Gothic, Colorado

*(Received 4 August 2007;
acceptance 18 February 2008; published online 11 July 2008; MS. number: A08-00065R2)*

The function and structure of alarm signals may vary with the caller's age, and some of this variation may be because young may have to attract the attention of their caregivers. The structure of calls may reveal this function. Yellow-bellied marmot, *Marmota flaviventris*, pups utter a novel vocalization, an elongated scream, which often contains nonlinear acoustic characteristics, 6% of the time when handled within about a week of emergence from their natal burrow. With a single exception in over 4000 captures, only pups uttered these unique vocalizations. Acoustically, pup screams are more than an order of magnitude longer than pup alarm calls and a majority of the screams have at least one type of nonlinearity. Playback experiments showed that average-length screams elicited higher-level responses than adult alarm calls and that elongated and average-length screams elicited higher-level responses than shortened screams. The acoustic structure of screams makes them especially evocative, and they may function to allow pups to recruit their mothers to help them fend off predators. More generally, an examination of nonlinearities in vocalizations of other species suggests that nonlinearities may be an honest indicator of arousal, and this honesty elicits heightened responses in receivers.

© 2008 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Keywords: alarm call; honest signal; *Marmota flaviventris*; nonlinear vocalization; yellow-bellied marmot

How do highly vulnerable neonates gain the attention of their parents or other caregivers when threatened? Darwin (1872) noted that young animals may scream and suggested that screams are a call for assistance. Screams in some species are uttered when individuals are highly aroused or in imminent danger and may elicit help from others (Gouzoules et al. 1984; Held et al. 2006). Are screams, then, simply typical alarm calls or are they different in some way?

We know that individuals of many species utter alarm calls and that the structure and function of these signals may vary with the caller's age. For instance, young animals, because of their small size and naïveté, may be vulnerable to a larger set of predators than adults and thus may be more likely to utter calls to a variety of stimuli (Cheney & Seyfarth 1990). By contrast, young animals may be relatively safe in their nests or dens and thus may be less likely to utter alarm calls in certain circumstances than adults (Magrath et al. 2006). Younger animals may also use calls to manipulate the behaviour of potential caregivers (Owings & Morton 1998), possibly as a means to learn about the true risk of different stimuli (Cheney & Seyfarth 1990; Mateo & Holmes 1997), whereas older animals may simply communicate risk to their young or similar-aged conspecifics (Blumstein 2007a). Young animals may thus be selected to produce different alarm vocalizations compared to adults.

Screams are produced when young are threatened (Gouzoules et al. 1984; Held et al. 2006). Arousal levels influence both the probability of uttering alarm calls (Blumstein et al. 2006c) and the structure of these vocalizations (Manser et al. 2002). For instance, meerkat, *Suricata*

Correspondence: D. T. Blumstein, Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA 90095-1606, U.S.A. (email: marmots@ucla.edu). L. Cooley is at the Rocky Mountain Biological Laboratory, Box 519, Crested Butte, CO 81224, U.S.A.

0003−3472/08/$34.00/0

© 2008 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

suricata, alarm calls vary in their overall structure to communicate risk and vary in the presence of nonlinearities (mostly deterministic chaos) to communicate urgency (Manser 2001; Manser et al. 2001).

Nonlinearities, such as warbles, subharmonics, biphonation and deterministic chaos, are a relatively understudied class of acoustic characteristics (Fitch & Hauser 2002) that may be present in mammalian (Wilden et al. 1998), amphibian (Suthers et al. 2006) and avian (Beckers & ten Cate 2006) vocalizations. Nonlinearities have been hypothesized to be particularly evocative and difficult to habituate to (Fitch & Hauser 2002). For instance, baby cries and screams are especially good at eliciting responses because of their unpredictability (Fitch et al. 2002). Thus, we may expect alarm vocalizations from juvenile animals to contain nonlinear elements.

We describe pup screams, an alarm vocalization uttered only by juvenile yellow-bellied marmots, *Marmota flaviventris*. These mostly tonal vocalizations contain a variety of nonlinear phenomena, and thus they should be particularly evocative to receivers. Because adult yellow-bellied marmots produce conspecific alarm calls (Blumstein & Armitage 1997), and because pup alarm calls may function to elicit help from adults (Blumstein & Daniel 2004), we conducted a series of playback experiments designed to identify the salience of these screams to older marmots. Screams varied in their duration, hence we synthesized screams and modified their duration to determine whether duration could influence responsiveness. We also asked whether pup screams were more evocative than alarm calls. The playback results, combined with a quantitative analysis of the structure of screams, suggest that screams are a novel vocalization designed to elicit aid from older marmots.

GENERAL METHODS

We conducted all studies with free-living yellow-bellied marmots in the East River Valley in and around the Rocky Mountain Biological Laboratory in Gunnison County, Colorado, U.S.A., a location where marmots have been studied since 1962 (Blumstein et al. 2006b). Social groups and social group membership are known. Detailed methods of marmot trapping and marking can be found in Armitage (1982). Briefly, we baited them with an handful of Omalene 100 horse food (Ralston Purina, Inc., St. Louis, Missouri, U.S.A.) into 10 × 12 × 32 inch Tomahawk live traps. We transferred the marmots into a conical handling bag through which we weighed the pups. We removed the pups from the handling bag and held each in one hand, during which time we plucked 20–30 hairs for subsequent paternity studies, inserted or checked ear tags for permanent identification, measured their left hindfoot and anogenital distance, marked them (if necessary) with a unique symbol for identification from afar using Nyanzol fur dye, collected any excreted faecal samples for parasitological and endocrinological studies and recorded any pup screams. The entire handling process took 5–10 min, after which we released the subject at the point of capture. Nonpups also may, if they were not captured in the past 2 weeks, have had up to a 2-ml blood sample taken from their femoral vein immediately after being transferred into the handling bag. We held nonpups in the handling bag and took a little longer to handle them (10–15 min); we released them too after taking all measurements and samples. We studied these marmots under a research protocol, ARC 2001-191-01, approved by the UCLA Animal Care Committee on 13 May 2002 and renewed annually, and trapped them under permits issued by the Colorado Division of Wildlife.

Between 2001 and 2005, 6% of the times when a pup was initially trapped, it screamed (25/416 initial trappings). In three instances, pups did not scream the first time they were trapped, but screamed on a subsequent trapping. One individual screamed both at the first trapping and on a subsequent trapping. We noted a total of 29 bouts of screams from pups: with only a single exception in over 4000 captures, older marmots did not utter this unique vocalization. Pups that screamed had emerged from their natal burrow an average of 1 week before (range 0–22 days from emergence, $\overline{X} \pm \mathrm{SD} = 6.8 \pm 6.2$ days). Unlike alarm calls uttered by pups, this scream was uttered only while being directly handled. No pups screamed while in the trap. Although not specifically counted, when pups screamed, they typically screamed more than once. This allowed us time to record multiple scream exemplars from most pups that uttered this vocalization.

SPECIFIC QUESTIONS

The Acoustic Structure of Pup Screams

Methods

We recorded 506 individual screams from 23 different subjects. Between 2001 and 2005, we recorded screams onto Sony PCM-M1 digital audiotape recorders, digitized them at 16 bits, 44 kHz, and later normalized them to 95% of peak amplitude. In 2006, we acquired screams directly (16 bits, 44 kHz) onto Marantz PMD 660 direct-to-disk recorders. We edited screams into individual AIF files and normalized them to 95% of peak amplitude before making any measurements.

Using Canary (Charif et al. 1995), we generated a spectrum and spectrogram for each of the normalized screams (spectrum: Hamming window, FFT size 512, overlap 98.44%, filter bandwidth 349.70 Hz, grid resolution time 0.1814 ms, frequency grid resolution 86.13 Hz, clipping level −120 dB; spectrogram: Hamming window, FFT size 512, overlap 98.44%, filter bandwidth 349.70 Hz, grid resolution time 0.1814 ms, frequency grid resolution 86.13 Hz, clipping level −120 dB). A single observer (D.T.R.) made all spectrogram measurements on the top 40 dB of each scream.

We selected up to 10 screams with the best signal-to-noise ratio from each individual to be analysed. For eight individuals with fewer than 10 screams, all were analysed. Nonlinearities—particularly deterministic chaos—made quantifying certain tonal features of the screams difficult. Thus we used only screams for which the specific features listed below could be accurately measured and excluded screams with excessive deterministic chaos from analysis. Because other forms of nonlinearities did not interfere with measurements, we included these in the pool of analysed screams. Our data set consisted of 194 individual screams, grouped into bouts from a total of 23 different individual marmot pups.

We then measured a number of features from the waveform, spectrogram, and spectrum of these screams (Fig. 1). We measured scream duration and rise time from the waveform, whereas we recorded the bandwidth of the fundamental and the number of peaks in the fundamental from the spectrum. We measured the number of harmonics, dominant frequency and start, end, minimum, maximum and peak frequencies of the fundamental and first harmonic from the spectrogram.

We also examined the spectrogram for the presence of complex structures and nonlinearities (Fig. 2). These included warbles (rapid frequency shifts), subharmonics, additional spectral components between the harmonics (Fitch et al. 2002) and biphonation (sidebands adjacent to the harmonics, Riede et al. 2004). We observed a third nonlinearity, deterministic chaos—noted as broadband energy on the spectrogram with residual periodic energy (Fitch et al. 2002)—in some screams, but because it prevented accurate measurements of tonal features, we excluded those screams from the pool of measured screams.

We calculated averages for each individual and used these individual averages to describe the screams and to

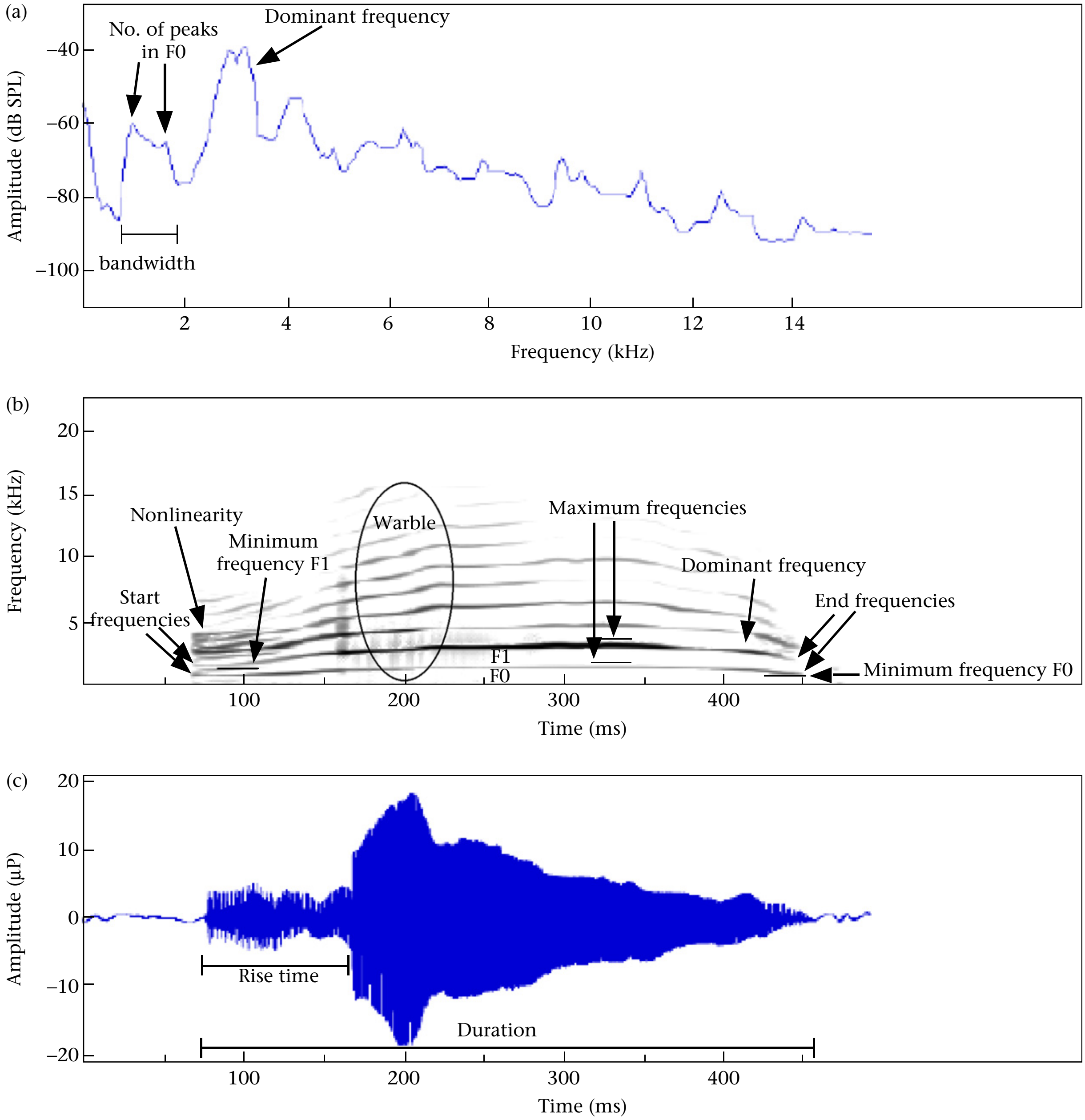

Figure 1. Acoustic measurements made on the yellow-bellied marmot pup scream. (a) Spectrum—bandwidth, number of peaks in the fundamental frequency. (b) Spectrogram—starting, ending, maximum, minimum and peak frequencies of fundamental and first harmonic; number of harmonics; presence and type of nonlinearities; presence of warbles; dominant frequency. (c) Waveform—rise time duration and scream duration.

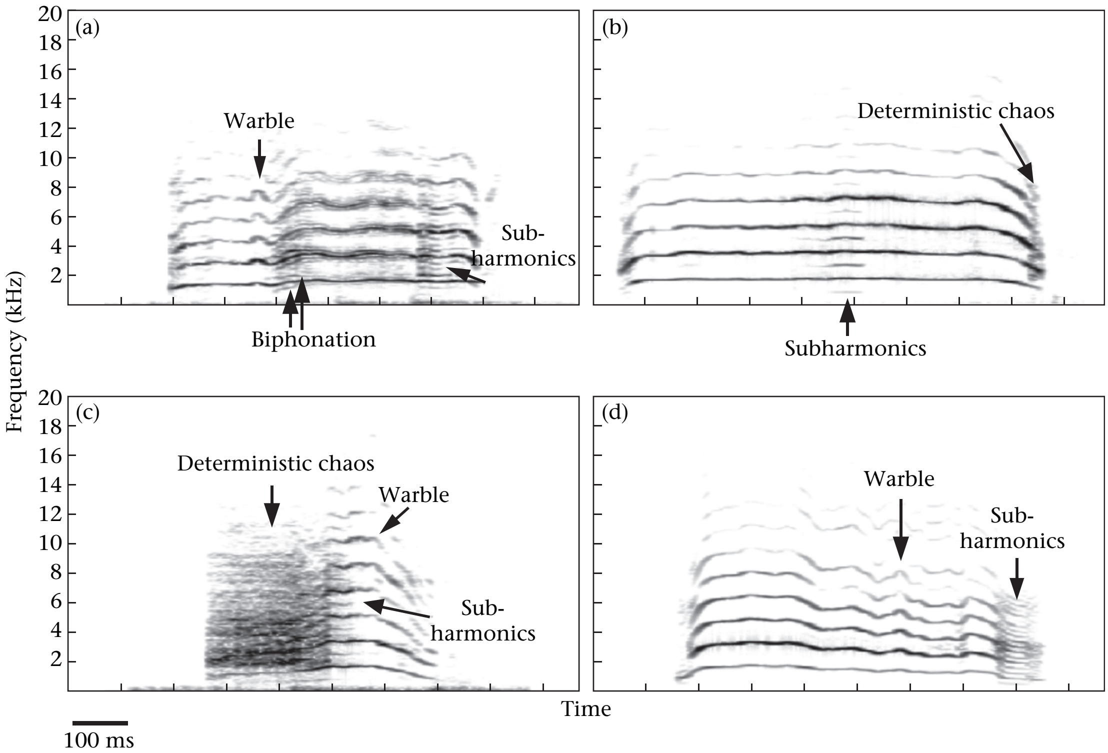

Figure 2. Spectrograms of marmot pup screams showing the various complexities and nonlinearities observed. (a) Biphonation, marked with arrows, appears as sidebands on the harmonics. (b) Subharmonics, marked by the arrow, are additional lines evenly spaced between harmonics. (c) Deterministic chaos, marked with bars, appears as sudden broadband noise. (d) Warbles, a complexity marked with arrows, are frequency discontinuities often associated with a change in amplitude. (a–d) All examples show bifurcations, a transition between the normal call and the various nonlinearities or between different types of nonlinearities.

compare them (using a Mann–Whitney *U* test) to averages from a sample of alarm calls from 11 different juveniles (10 calls each, except for two individuals for which there were only five available calls) that had previously been measured (Blumstein & Munos 2005). We averaged the percentage of screams containing subharmonics, biphonation and warbles for each bout and used this average to calculate a total average percentage for all screams.

The individual screams were also subjected to discriminant function analysis to determine whether the measured variables allowed screams to be assigned to individual pups. For these analyses, we analysed screams from 18 different subjects that each uttered 9 or 10 (mode = 10) calls.

Results

Pup screams were significantly different from pup alarm calls in all measured dimensions (Table 1). They were substantially longer and they included a number of nonlinearities. In addition to deterministic chaos, 55% of screams had subharmonics, 13% had biphonation and 74% had warbles. Although not quantified during trapping, on some occasions when a pup screamed, adult marmots approached the person holding the pup. On rare events the approaching adult uttered alarm calls. Discriminant function analysis correctly classified 60.1% of calls to an individual, a value that was substantially more than the 5.5% correct classification that was expected by chance. Frequency characteristics were particularly useful in the discrimination (Table 2).

The Meaning and Function of Pup Screams

Methods

We conducted two experiments to study the function of pup screams. The first experiment, conducted in 2004, asked whether scream duration influenced responsiveness. The second experiment, conducted in 2005, asked whether pup screams were more salient than alarm calls (i.e. whether they elicited greater responses).

Based on a preliminary analysis of pup screams recorded in 2001 and 2002, and before we realized that there were a variety of nonlinearities in the screams, we used Signal 3.0 (Engineering Design, Inc., Belmont, Massachusetts, U.S.A., 1989) to synthesize tonal pup screams that had identical frequency contours (all contained warbles) and differed only in length. Our preliminary analysis examined 230 individual pup screams recorded from 14 individuals for the duration of screams ($\overline{X} \pm \text{SD} = 489 \pm 155$ ms; range 90–1607 ms) and the internote interval between screams ($\overline{X} \pm \text{SD} = 298 \pm 99$ ms; range 33–1094 ms). We created average-duration screams (490 ms), as well as screams that were 2 standard deviations longer (800 ms) and shorter (180 ms) than the average duration. To do so, we chose four exemplars of screams from each of four

Table 1. Comparison of the mean (±SE) of bout averages for rise time, call duration and start, end, peak, minimum and maximum frequencies of both the fundamental and the first harmonic between marmot pup screams and marmot juvenile calls

Feature	Alarm call ($\bar{X} \pm$ SE)	Scream ($\bar{X} \pm$ SE)	*P*
Duration (ms)	37.26±1.31	459.80±10.81	<0.0001
Rise time (ms)	1.36±0.05	40.56±1.66	<0.0001
F0 start frequency (kHz)	3.39±0.09	1.20±0.02	<0.0001
F0 end frequency (kHz)	2.94±0.10	1.10±0.02	<0.0001
F0 peak frequency (kHz)	3.63±0.11	1.97±0.02	<0.0001
F0 minimum frequency (kHz)	2.58±0.09	0.88±0.02	<0.0001
F0 maximum frequency (kHz)	4.15±0.12	2.26±0.02	<0.0001
F1 start frequency (kHz)	6.83±0.20	2.52±0.04	<0.0001
F1 end frequency (kHz)	5.68±0.25	2.31±0.03	<0.0001
F1 peak frequency (kHz)	6.83±0.26	3.60±0.05	<0.0001
F1 minimum frequency (kHz)	5.32±0.25	1.99±0.02	<0.0001
F1 maximum frequency (kHz)	7.85±0.25	4.30±0.04	<0.0001

P Values from Mann–Whitney *U* tests.

individuals (16 screams total, 4 per individual) that were similar in duration to the average (range 395–585 ms) and of good quality. We then adjusted the length of each scream (including harmonic structure) to be average, long, or short by stretching or shrinking the frequency contour in time accordingly (Fig. 3). Each playback was composed of the four exemplars per individual separated by 300- to 500-ms internote intervals, where the exemplars within a playback were all of average, short, or long duration. The responses to these synthesized screams were compared to one of four playbacks composed of four adult female alarm calls (four exemplars per individual within a series) separated by 400- to 500-ms internote intervals. For the 2005 experiment, we used the synthesized average pup screams and eight sets of four-note alarm calls from eight different adult females (four exemplars per individual) and eight sets of four-note pup alarm calls from eight different pups (four exemplars per individual). We used eight different four-note conspecific alarm call series (a relatively high-risk alarm), to ensure that marmots heard alarm calls from unfamiliar animals from different social groups.

We broadcast vocalizations as uncompressed AIF files using an iPod (Apple Computer, Cupertino, California, U.S.A.) through a powered speaker (Advent AV 570; Recoton Home Audio, Benici, California, U.S.A.).

We baited marmots with a handful of Omolene 300 horse feed (Ralston Purina) to a location 1–2 m from their burrow. For all experiments, we broadcast calls to nonpups (i.e., yearlings and adults). We have no evidence to suggest that systematic differences exist in how these different age–sex categories respond to playbacks.

Does scream duration influence responsiveness? In the 2004 experiment, we broadcast adult female alarm calls and shortened, average and lengthened pup screams to 15 subjects (nine adult females, one adult male, three yearling females, two yearling males) in five groups (Marmot Meadow Aspen, Marmot Meadow Main Talus, River South, River Spruce, Gothic Townsite). We exposed each subject to all four stimuli, typically no more than one per day ($\bar{X} \pm \mathrm{SD} = 27.27 \pm 21.91$ h between playbacks, median = 24.08 h, range 0.070–120.25 h). Each subject heard average, shortened and lengthened pup screams derived from the same individual. Although we aimed to have each subject hear only playbacks specifically directed at that individual, subjects sometimes heard playbacks directed at other individuals in addition to their own. In all but three cases it happened when we were targeting another subject and a nontarget subject suddenly appeared at the bait just as we started recording the preplayback baseline period. In most cases, we aborted the playbacks. However, in nine cases, we did not (because we were trying to complete a series of playbacks on a subject). We could find no systematic bias in those subjects that heard more than a single playback in a day. Having an animal hear a playback and not quantifying its behaviour creates some difficulties because the animals are likely to habituate to repeated

Table 2. Standardized canonical discriminant function coefficients that classify pup screams to the vocalizing individual

	Discriminant functions					
	1	2	3	4	5	6
Call duration (ms)	−0.33	0.132	−0.592	−0.34	0.078	0.662
F0 bandwidth (kHz)	−0.458	−0.788	1.106	0.369	−0.218	1.051
N harmonics	−0.15	0.409	−0.089	0.471	0.933	−0.053
Maximum frequency of F0 (kHz)	1.287	0.324	−1.415	0.082	0.793	−0.827
Starting frequency F1 (kHz)	−0.481	−0.288	0.983	−0.742	0.266	0.206
Ending frequency F1 (kHz)	0.205	0.678	0.684	0.231	−0.141	0.56
Percentage of variance explained by discriminant function	47.7	20.2	14.9	10.2	4.2	2.7

A total of 60.1% of the screams were correctly classified. Variables not included after stepwise deletion comprised rise time duration, dominant frequency, *N* peaks in F0, *N* with complex ending, starting frequency of F0, ending frequency of F0, peak frequency of F0, minimum frequency of F0, peak frequency of F1 and maximum frequency of F1.

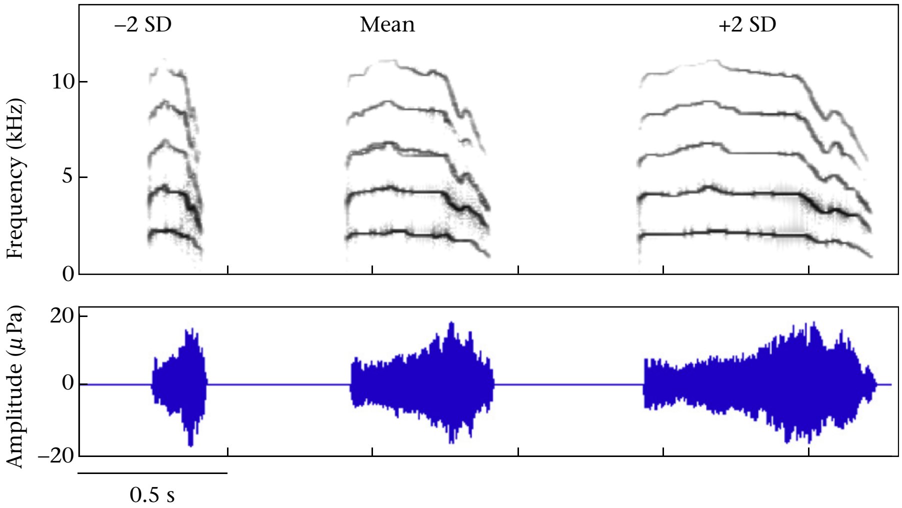

Figure 3. Waveform and spectrogram of three synthesized pup screams that were −2 SD below the mean duration, the mean duration, and +2 SD above the mean duration of pup screams. The vocalizations were synthesized in Signal 3.0 (Engineering Design 1998). Spectrogram parameters: 1024 point frame length and FFT with 99.8% overlap.

exposures to the experimental set-up. Assuming that a subject that elected to forage at the bait was 'relaxed' enough to be exposed to another stimulus, we elected to keep these observations. Overall, 9/15 subjects heard all of their playbacks at least one day apart in this experiment. If we analyse only those subjects, we see overall patterns and moderate to large effect sizes that are similar to those reported under Results, but, because of the smaller sample size, we lose some statistical significance. On average, subjects heard $\overline{X} \pm$ SD = 2.20 ± 1.74 playbacks prior to each playback directed at that individual (median = 2, range 0–7). Likewise, we aimed to target solitary subjects; however, there were sometimes other individuals present, either at the bait or within the vicinity (50 m) of the subject. There were an average of 0.65 ± 0.76 others present at the bait during playback (median = 0, range 0–2). On average, there were 1.53 ± 1.48 others present within 50 m of the subject, including those at the bait (median = 1, range 0–6).

Are pup screams more evocative than alarm calls? In the 2005 experiment, we broadcast the three stimuli (average-length scream, adult alarm call, pup alarm call) to 14 different subjects (seven adult females, three adult males, four yearling females) in four groups (Marmot Meadow Aspen, River South, River Spruce, Gothic Townsite). We exposed each subject to all three stimuli, typically no more than one per day ($\overline{X} \pm$ SD = 67.08 ± 123.21 h between playbacks, median = 24.01, range 0.070–429.53 h). Although we aimed to have each subject hear only playbacks specifically directed at that individual, subjects sometimes heard playbacks directed at other individuals in addition to their own. On average, subjects heard $\overline{X} \pm$ SD = 1.07 ± 0.94 playbacks prior to each playback directed at that individual (median = 1, range 0–3). Likewise, we aimed to target solitary subjects; in this experiment, there were no others at the bait during any of the playbacks, and there were only two cases in which there was another individual within 50 m of the subject during playback. As before, if we eliminated the two subjects who heard playbacks in the same day (one was an alarm call, the other was a pup scream), we obtained results similar to those we report below.

Additional playback considerations and analysis. For both experiments, the order of stimulus presentation was counterbalanced to control for order effects. Once an animal was foraging at the bait, we started the 2-min sound track was started. We played back normalized screams and alarm calls at 95 dB SPL (measured at 1 m) from a speaker placed 10–12 m from the bait. Each sound track started with 1 min of silence, to obtain baseline time allocation for an individual. This was followed by an additional minute, with the playback commencing at the beginning of this period and lasting from 1.5 to 4.5 s. We observed and videorecorded foraging marmots with a Cannon GL-1 mini-DV digital video recorder at distances that did not obviously affect their behaviour (40–80 m, depending upon the individual and the terrain).

For both experiments, we scored videotapes using the event recorder JWatcher (Blumstein et al. 2006a; Blumstein & Daniel 2007). We noted the onset of bouts of foraging, standing quadrupedally and looking, rearing up bipedally and looking, walking, running, self-grooming, interacting socially and time spent in burrow and time spent out of sight. We calculated the proportion of time allocated to foraging, heightened vigilance (rearing and looking), total vigilance (stand-looking and rear-looking), locomotion (walking and running) and staying in the burrow. Although we visually explored all the data, the proportion of time allocated by individuals to foraging was our primary assay, because all subjects foraged before playback and responded to the playback by decreasing foraging. After playback, marmots primarily traded off foraging with vigilance, but they also spent some time in locomotion or inside their burrow. We analysed time allocation primarily in the first 15 s of playback, because responses to acoustic stimuli were brief and subjects mostly resumed their initial behaviour within a minute.

For each playback, we subtracted time allocation following stimulus presentation from the 1-min baseline period to determine whether there was a significant response to the stimulus. We calculated 95% confidence intervals of the difference from baseline and interpreted those significantly different from zero as indicating a response to the stimulus. We then fitted repeated-measures general linear models to explain variation in the proportion of time spent foraging and the proportion of time spent engaged in high vigilance combined with the proportion of time spent in the burrow (hereafter high vigilance plus burrow) during the first 15 s of playback. We used an angular transformation (appropriate for proportions) to approximate more closely a normal distribution for each of these variables. We used Mauchly's test to test for sphericity (Keppel 1991); in cases for which we rejected the hypothesis of sphericity, we report Huynh–Feldt corrected P values and Huynh–Feldt corrected degrees of freedom.

For multiple comparisons we calculated sequential Bonferroni P critical values (Holm 1979; Rice 1989) and set our experimentwise significance level at 5%. For the 2004 experiment, we were interested in comparing the average-length pup screams to their shortened counterparts, their lengthened counterparts, and adult alarm calls. Therefore, we divided 0.05 by 3 to obtain a P critical value of 0.017 for the first comparison; we divided 0.05 by 2 to obtain a P critical value of 0.025 for the second comparison and we used 0.05 as the P critical value for the third comparison. For the 2005 experiment, we made all possible comparisons for a total of three comparisons (i.e. P critical $= 0.017$ for the first comparison, P critical $= 0.025$ for the second comparison and P critical $= 0.05$ for the third comparison).

We tested for order effects by fitting a repeated-measures general linear model focusing on the first 15 s of playback in which the playback order, rather than the playback stimulus, was the factor. Finally, we regressed the number of previous playbacks heard and the number of other individuals aboveground and within 50 m of the focal subject during the playback against our dependent variables: the angular transformation of the proportion of time spent foraging and the angular transformation of the proportion of time spent in high vigilance plus burrow.

For all experiments we calculated partial η^2 as a measure of effect size for general linear models, and Cohen's d as a measure of effect size for pairwise comparisons, using the pooled standard deviation (Cohen 1988). By tradition, small effects are inferred when $d = 0.2$, medium effects when $d = 0.5$, and large effects when $d = 0.8$ (Cohen 1988). We calculated all statistics in SPSS 13.0 for the Macintosh (SPSS, Inc., Chicago, Illinois, U.S.A., 2002).

Results

Does scream duration influence responsiveness? After hearing all playback stimuli, marmots responded by significantly decreasing foraging during the first 15 s that included and immediately followed the playback (95% confidence intervals for difference from baseline in proportion of time spent foraging: adult alarm call: −0.421 to −0.068; average scream: −0.619 to −0.384; lengthened scream: −0.495 to −0.266; shortened scream: −0.421 to −0.180). Marmots significantly increased the proportion of time spent rear-looking or in the burrow compared to baseline after hearing all playback stimuli during the first 15 s that included and immediately followed the playback (95% confidence intervals for high vigilance plus burrow: adult alarm call: 0.094–0.520; average scream: 0.208–0.655; lengthened scream: 0.110–0.580; shortened scream: 0.00–0.400).

Marmots differed in response to the four treatment groups in proportion of time spent foraging ($F_{3,42} = 3.692$, $P = 0.019$, partial $\eta^2 = 0.209$) but not for high vigilance plus burrow ($F_{3,42} = 0.969$, $P = 0.416$, partial $\eta^2 = 0.065$). Marmots foraged significantly and substantially less after hearing average-length pup screams compared to adult alarm calls ($P = 0.011$, P critical $= 0.017$, $d = 0.949$) or shortened pup screams ($P = 0.021$, P critical $= 0.025$, $d = 0.758$). There was no difference in foraging in response to average-length pup screams compared with lengthened pup screams ($P = 0.566$, P critical $= 0.05$, $d = 0.186$).

There were no significant effects of order during the first 15 s of playback for foraging ($F_{3,42} = 0.999$, $P = 0.403$, partial $\eta^2 = 0.067$) or high vigilance plus burrow (H–F corrected: $F_{2.466,34.518} = 1.346$, $P = 0.275$, partial $\eta^2 = 0.088$).

There was no significant difference in the proportion of time spent foraging during baseline periods among the four treatment groups ($F_{3,42} = 1.701$, $P = 0.181$, partial $\eta^2 = 0.108$). There was no difference in the proportion of time spent in high vigilance plus burrow during baseline periods among the four treatment groups (H–F corrected: $F_{1.644,23.019} = 0.817$, $P = 0.432$, partial $\eta^2 = 0.055$).

There was a significant positive relationship between the number of previous playbacks heard and the proportion of time spent foraging in the first 15 s of playback ($R_{59} = 0.266$, $P = 0.040$). However, when two outlier points were removed (number of playbacks heard was 6 in one case and 7 in another), this relationship disappeared ($R_{57} = 0.198$, $P = 0.137$). Likewise, there was a significant negative relationship between the number of previous playbacks heard and the proportion of time spent in high vigilance plus burrow in the first 15 s of playback ($R_{59} = 0.276$, $P = 0.033$). However, when two outlier points were removed (number of playbacks heard was 6 in one case and 7 in another), this relationship also disappeared ($R_{57} = 0.232$, $P = 0.137$). Removing these outliers did not affect the main conclusions of our study.

Only a small amount of variation was explained by the number of other individuals aboveground and within 50 m of the subject and the proportion of time spent foraging ($R_{59} = 0.239$, $P = 0.066$). There was no relationship between the number of other individuals aboveground and within 50 m of the subject and the proportion of time spent in high vigilance plus burrow ($R_{59} = 0.173$, $P = 0.185$).

Are pup screams more evocative than alarm calls? After hearing all playback stimuli, marmots responded by significantly decreasing foraging during the first 15 s that included and immediately followed the playback (95%

confidence intervals for difference from baseline in proportion of time spent foraging: adult alarm call: −0.558 to −0.286; pup alarm call: −0.552 to −0.230; average pup scream: −0.657 to −0.292). Marmots significantly increased the proportion of time spent rear-looking or in the burrow compared to baseline after hearing pup alarm calls and average pup screams, but not adult alarm calls, during the first 15 s that included and immediately followed the playback (95% confidence intervals for high vigilance plus burrow: adult alarm call: −0.067 to 0.353; pup alarm call: 0.086 to 0.574; average pup scream: 0.271 to 0.750).

In this experiment, marmots did not vary their responses among the three stimuli during the first 15 s that included and immediately followed the playback (H−F corrected: $F_{1.374,17.867} = 0.365$, $P = 0.621$, partial $\eta^2 = 0.027$). Nor was there any difference in high vigilance plus burrow for this same period ($F_{2,26} = 1.660$, $P = 0.210$, partial $\eta^2 = 0.113$).

However, a visual examination of the data suggested that the response persisted over the subsequent 45 s for the pup screams but did not persist either for the adult or for the pup alarm calls. We thus further analysed the 45-s period immediately following the first 15 s of the playback. We found a significant difference in foraging response among the treatments ($F_{2,26} = 4.378$, $P = 0.023$, partial $\eta^2 = 0.252$). Marmots had a significantly greater response to the pup scream compared to the adult alarm call ($P = 0.015$, P critical $= 0.017$, $d = 0.905$). There was no difference in foraging response between adult alarm calls and pup alarm calls ($P = 0.678$, $d = 0.098$), although there was a large but not significant difference comparing pup screams to pup alarm calls ($P = 0.077$, $d = 0.742$). There was no difference in response among the treatments for high vigilance plus burrow in the subsequent 45 s ($F_{2,26} = 2.303$, $P = 0.120$, partial $\eta^2 = 0.151$).

These results are in contrast to previously published results (Blumstein & Daniel 2004): yellow-bellied marmot pup alarm calls were not more evocative than calls from adults in the present study. The difference may lie in the structure of the playback. In the previous study, each playback comprised a short burst of four alarm calls (with internote intervals similar to those of the current study's playbacks) followed by five more calls played at 10-s intervals throughout the entire minute of playback. The current study (like other recent experiments) used the initial short burst of four calls only. Both studies found no difference in the initial response to the short burst of calls; however, the previous study found that the response persisted over the entire minute of playback for the pup calls but not the adult calls. In both experiments the time of year in which we conducted the experiments was similar (22 July through 8 August for the previous experiment, 5 through 24 July for the current experiment). Importantly, pups had emerged from the burrows and were aboveground in both studies. The composition of subjects was also similar for both studies (eight adult females, two adult males, three yearling females for the previous study, and seven adult females, three adult males, four yearling females for the current study). In both studies a similar proportion of subjects were mothers (five adult females for the previous experiment, and six adult females for the current study). Further study will be required to explain this discrepancy conclusively.

There was no difference in the proportion of time spent foraging during baseline periods among the three treatment groups ($F_{2,26} = 0.365$, $P = 0.698$, partial $\eta^2 = 0.027$). There was no difference in the proportion of time spent in high vigilance plus burrow during baseline periods among the three treatment groups (H−F corrected: $F_{1.000,13.000} = 1.000$, $P = 0.336$, partial $\eta^2 = 0.071$; note that marmots did not engage in any high vigilance plus burrow for two of the three treatments during the baseline minute).

There was no effect of order for foraging during the first 15 s that included and immediately followed the playback (H−F corrected: $F_{1.466,19.057} = 0.962$, $P = 0.374$, partial $\eta^2 = 0.069$). Similarly, there was no effect of order for foraging during the subsequent 45 s ($F_{2,26} = 0.065$, $P = 0.937$, partial $\eta^2 = 0.005$). There was no effect of order for high vigilance plus burrow during the first 15 s that included and immediately followed the playback ($F_{2,26} = 0.429$, $P = 0.656$, partial $\eta^2 = 0.032$). Similarly, there was no effect of order for the subsequent 45 s for high vigilance plus burrow ($F_{2,26} = 1.778$, $P = 0.189$, partial $\eta^2 = 0.120$).

Because other individuals were rarely present aboveground during the playbacks, we did not regress response against number of others within the vicinity of the subject. There was no effect of number of previous playbacks heard on the foraging response in the first 15 s of playback ($R_{41} = 0.092$, $P = 0.561$) nor was there any effect in the subsequent 45 s ($R_{41} = 0.029$, $P = 0.855$). There was no effect of number of previous playbacks heard on the high vigilance plus burrow response in the first 15 s of playback ($R_{41} = 0.094$, $P = 0.555$) nor was there any effect in the subsequent 45 s ($R_{41} = 0.008$, $P = 0.567$).

DISCUSSION

Yellow-bellied marmot pups occasionally utter a unique vocalization, which we denote as a scream, within a week of emerging from their natal burrow. At this time, they are typically less than 500 g and are highly vulnerable to predators. The structure of these screams is significantly different from alarm calls uttered by pups with respect to all call features compared. In addition to these distinct differences in tonal qualities, most pup screams contain nonlinear vocal phenomena, whereas alarm calls do not, and they contain a substantial amount of potential information about caller identity. Marmots responded more to screams than to adult alarm calls and more to longer or average-duration screams than to shorter screams. Uniquely, adult yellow-bellied marmots (2/3 were known to be the screamer's mother) occasionally uttered alarm calls in response to hearing a pup scream. This sort of response never happened in hundreds of previous playbacks of alarm calls to yellow-bellied marmots. Taken together, screams therefore have a conspecific warning function and they may serve to recruit help from adults, potentially the screamer's mother, as seen in some other species (Gouzoules et al. 1984; Held et al. 2006).

Screams seem to contain a substantial amount of information about the identity of the vocalizer. A stronger demonstration of this would have required us to have recordings from different occasions, something that was impossible because of the low frequency with which pups screamed and because those pups that did scream almost always did so only the first time they were caught. None the less, if screams functioned to recruit help from adults, we would expect that they might be targeted to their parents, who presumably would be able to identify their pups acoustically. Adult yellow-bellied marmots are able to discriminate among adult callers based solely on their vocalizations (Blumstein & Daniel 2004; Blumstein 2007b).

The structure of screams suggests that they could also be a protean display (Caro 2005) towards their predators. The lower frequency of the pup screams with the addition of the nonlinear subharmonics may also act to discourage predation. Many animals associate lower pitched calls with larger body size. By making lower frequency screams, with subharmonics—which can lower the apparent pitch of the call without requiring the physiological means to produce a normal low-frequency call (Fitch et al. 2002)—a threatened pup might be able to convey the acoustic illusion that it is larger than its actual size, thus discouraging a potential attacker.

If pup screams were indeed protean displays, we would expect that predators might occasionally release a screaming pup. Observing predation at our study site is rare, but we have observed a few successful kills by a female red fox, *Vulpes velox*. In no case did screams prevent the fox from killing the pup. One pup apparently survived by being still and escaping after the fox either cached the still-alive marmot pup or gave it to her kits. Future observations will be needed to determine whether pups have any chance of escaping their predators by screaming.

Marmot pup screams contain warbles, subharmonics, biphonation and deterministic chaos in a variety of combinations. Some screams had no nonlinearities, whereas others had several bifurcations—transitions between the different complexities and/or nonlinearities (Fitch et al. 2002)—within one call. Pup screams are unique in that they are the only marmot alarm vocalizations, with the possible exception of the quiet and rarely uttered ‘chucks’ (Blumstein & Armitage 1997), to contain nonlinearities. Nonlinearities are produced by the different interactions of two or more oscillators—such as the right and left vocal folds or other such anatomical structures (Wilden et al. 1998). These interactions result in synchronization at different frequencies, which can lead to subharmonics or biphonation, or in desynchronization, which can lead to deterministic chaos. Asymmetries in the vocal folds are one feature that can lead to desynchronized vibrations or differing vibratory frequencies—and consequently to nonlinearities (Fitch et al. 2002). It is possible that some feature of a marmot pup’s developing vocal folds, such as asymmetry, is responsible for these nonlinearities, whereas more developed vocal folds of marmots produce regular phonation.

It is also possible that highly aroused pups have less control over their vocal apparatus and thus sometimes produce vocalizations with deterministic chaos. Pups, because of their size and naïveté, are particularly vulnerable to predators. Highly aroused meerkats communicate relative risk in their functionally referential alarm calls by adding what seems to be deterministic chaos to their calls (Manser 2001). Highly aroused chimpanzees, *Pan troglodytes*, add nonlinearities to their pant-hoots (Riede et al. 2004). And, piglets, *Sus scrofa*, Japanese macaques, *Macaca fuscata*, and domestic dogs, *Canis familiaris*, all produce nonlinearities when highly aroused (Tokuda et al. 2002).

The ability to produce nonlinearities may also be advantageous to a marmot pup in different ways. The presence of complex structure and nonlinearities allows for complex and unpredictable calls (Fitch et al. 2002). This additional complexity and variation might allow individual callers to be identified more readily and is supported by the high degree of individuality that seems to be present in the pup screams. The unpredictability that nonlinearities provide in these screams could be advantageous to threatened marmot pups because it prevents listeners from habituating to their screams—supporting the idea of a possible protean display. Consistent with this hypothesis are the observations that screams are produced when the pups are under direct threat, normal alarm calls are tonal and do not contain these nonlinear features, and screams tend to be more varied than alarm calls with respect to duration and rise time. Thus, these screams are also likely to be an honest indicator of threat.

Acknowledgments

Partial support for this research came from NSF-DBI-0242960 (to the Rocky Mountain Biological Laboratory), the Unisense Foundation, UCLA Faculty Senate Faculty Research Grants, a UCLA Assistant Professor’s Initiative Grant, and the UCLA Division of Life Sciences Dean’s Recruitment and Retention Funds (to Blumstein). Cooley was a NSF-REU Fellow. We thank all the marmoteers, for keeping marmots marked and identified as well as for frantically turning on recorders to capture these screams, and Mike Breed, Lee Drickamer and an anonymous referee for very constructive comments that helped us clarify and broaden our message.

References

Armitage, K. B. 1982. Yellow-bellied marmot. In: *CRC Handbook of Census Methods for Terrestrial Vertebrates* (Ed. by D. E. Davis), pp. 148–149. Boca Raton, Florida: CRC Press.

Beckers, G. J. L. & ten Cate, C. 2006. Nonlinear phenomena and song evolution in *Streptopelia* doves. *Acta Zoologica Sinica, Supplement*, **52**, 482–485.

Blumstein, D. T. 2007a. The evolution of alarm communication in rodents: structure, function, and the puzzle of apparently altruistic calling in rodents. In: *Rodent Societies* (Ed. by J. O. Wolff & P. W. Sherman), pp. 317–327. Chicago: University of Chicago Press.

Blumstein, D. T. 2007b. The evolution, function, and meaning of marmot alarm communication. *Advances in the Study of Behavior*, **37**, 371–400.

Blumstein, D. T. & Armitage, K. B. 1997. Alarm calling in yellow-bellied marmots. I. The meaning of situationally-specific calls. *Animal Behaviour*, **53**, 143–171.

Blumstein, D. T. & Daniel, J. C. 2004. Yellow-bellied marmots discriminate between the alarm calls of individuals and are more responsive to the calls from juveniles. *Animal Behaviour*, **68**, 1257–1265.

Blumstein, D. T. & Daniel, J. C. 2007. *Quantifying Behavior the JWatcher Way*. Sunderland, Massachusetts: Sinauer.

Blumstein, D. T. & Munos, O. 2005. Individual and age/sex class variation in marmot alarm calls. *Animal Behaviour*, **69**, 353–361.

Blumstein, D. T., Daniel, J. C. & Evans, C. S. 2006a. JWatcher 1.0. URL: <http://www.jwatcher.ucla.edu>.

Blumstein, D. T., Ozgul, A., Yovovitch, V., Van Vuren, D. H. & Armitage, K. B. 2006b. Effect of predation risk on the presence and persistence of yellow-bellied marmot (*Marmota flaviventris*) colonies. *Journal of Zoology*, **270**, 132–138.

Blumstein, D. T., Patton, M. L. & Saltzman, W. 2006c. Faecal glucocorticoid metabolites and alarm calling in free-living yellow-bellied marmots. *Biology Letters*, **2**, 29–32.

Caro, T. 2005. *Antipredator Defenses in Birds and Mammals*. Chicago: University of Chicago Press.

Charif, R. A., Mitchell, S. & Clark, C. W. 1995. *Canary 1.2 User's Manual*. Ithaca, New York: Cornell Laboratory of Ornithology.

Cheney, D. L. & Seyfarth, R. M. 1990. *How Monkeys See the World*. Chicago: University of Chicago Press.

Cohen, J. 1988. *Statistical Power Analysis for the Behavioral Sciences*. 2nd edn. Hillsdale, New Jersey: L. Erlbaum.

Darwin, C. 1872. *The Expression of the Emotions in Man and Animals*. London: John Murray.

Fitch, W. T. & Hauser, M. D. 2002. Unpacking ''honesty'': vertebrate vocal production and the evolution of acoustic signals. In: *Springer Handbook of Auditory Research* (Ed. by A. Simmons, R. R. Fay & A. N. Popper), pp. 65–137. New York: Springer.

Fitch, W. T., Neubauer, J. & Herzel, H. 2002. Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production. *Animal Behaviour*, **63**, 407–418.

Gouzoules, S., Gouzoules, H. & Marler, P. 1984. Rhesus monkey (*Macaca mulatta*) screams: representational signalling in the recruitment of agonistic aid. *Animal Behaviour*, **32**, 182–193.

Held, S., Mason, G. & Mendl, M. 2006. Maternal responsiveness of outdoor sows from first to fourth parities. *Applied Animal Behaviour Science*, **98**, 216–233.

Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, **6**, 65–70.

Keppel, G. 1991. *Design and Analysis: a Researcher's Handbook*. 3rd edn. Upper Saddle River, New Jersey: Prentice Hall.

Magrath, R. D., Platzen, D. & Kondo, J. 2006. From nestling calls to fledgling silence: adaptive timing of change in response to aerial alarm calls. *Proceedings of the Royal Society of London, Series B*, **273**, 2335–2341.

Manser, M. 2001. The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society of London, Series B*, **268**, 2315–2324.

Manser, M. B., Bell, M. B. & Fletcher, L. B. 2001. The information receivers extract from alarm calls in suricates. *Proceedings of the Royal Society of London, Series B*, **268**, 2485–2491.

Manser, M. B., Seyfarth, R. M. & Cheney, D. L. 2002. Suricate alarm calls signal predator class and urgency. *Trends in Cognitive Science*, **6**, 55–57.

Mateo, J. M. & Holmes, W. G. 1997. Development of alarm-call responses in Belding's ground squirrels: the role of dams. *Animal Behaviour*, **54**, 509–524.

Owings, D. H. & Morton, E. S. 1998. The role of information in communication: an assessment/management approach. *Perspectives in Ethology*, **12**, 359–390.

Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**, 223–225.

Riede, T., Owren, M. J. & Arcadi, A. C. 2004. Nonlinear acoustics in pant hoots of common chimpanzees (*Pan troglodytes*): frequency jumps, subharmonics, biphonation, and deterministic chaos. *American Journal of Primatology*, **64**, 277–291.

Suthers, R. A., Narins, P. M., Lin, W.-Y., Schnitzler, H.-U., Denziger, A., Xu, C.-H. & Feng, A. S. 2006. Voices of the dead: complex nonlinear vocal signals from the larynx of an ultrasonic frog. *Journal of Experimental Biology*, **209**, 4984–4993.

Tokuda, I., Riede, T., Neubauer, J., Owren, M. J. & Herzel, H. 2002. Nonlinear analysis of irregular animal vocalizations. *Journal of the Acoustical Society of America*, **111**, 2908–2919.

Wilden, I., Herzel, H., Peters, G. & Tembrock, G. 1998. Subharmonics, biphonation, and deterministic chaos in mammal vocalization. *Bioacoustics*, **9**, 171–196.