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

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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.

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*

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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, $\overline{X} \pm SD = 6.8 \pm 6.2$ 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