

Pups crying bass: vocal adaptation for avoidance of age-dependent predation risk in ground squirrels?

Vera A. Matrosova · Ilya A. Volodin ·
Elena V. Volodina · Andrey F. Babitsky

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Abstract In most mammals, larger adult body size correlates with lower fundamental frequency and more closely spaced formants in vocalizations relative to juveniles. In alarm whistles of two free-living rodents, the speckled ground squirrel *Spermophilus suslicus* and yellow ground squirrel *S. fulvus*, these cues to body size were absent despite prominent differences in body weight and skull and larynx sizes between juveniles and adults. No significant correlations were found between the individual maximum fundamental frequency and body weight, both within age classes and for pooled samples of all animals within species. Furthermore, the mean alarm whistle maximum fundamental frequencies did not differ significantly between age classes (juvenile versus adult) in the speckled squirrel and were even significantly lower in juvenile yellow squirrels. We discuss the hypothesis that the obfuscation of vocal differences between juvenile and adult squirrels may represent a special adaptation of pup vocal behaviour—a form of “vocal mimicry,” resulting in

imitation of adult vocal pattern to avoid infanticide and age-dependent predation risk.

Keywords *Spermophilus suslicus* · *Spermophilus fulvus* · Alarm call · Vocal mimicry · Infanticide · Antipredator behaviour

Introduction

In mammals, vocal cues to body size are attributed either to the formant or to the fundamental frequency. The fundamental frequency is determined by the sound source (specifically, by the vibratory frequency of vocal folds in the larynx), and further filtration of the source sound occurs in the supralaryngeal vocal tract (Fant 1960; Titze 1994). The most important determinant of formant frequencies is the length of the vocal tract (Fitch and Hauser 1995, 2002). In mammals, the vocal tract is anatomically rigidly related to the skull dimensions (Fitch and Hauser 2002), and strong correlations between the condylobasale skull length, the vocal tract osseous structures, and body weight have been reported (Fitch 2000). Therefore, the formant frequencies of vocalizations provide a good indicator of body size in adult mammals (Fitch 1997; Fitch and Giedd 1999; Riede and Fitch 1999).

Fundamental frequencies of calls provide another cue to body size in mammals (Morton 1977; Owings and Morton 1998). The call fundamental frequency is set by vibration of vocal folds, stretched across the tracheal aperture between the laryngeal cartilages and depends primarily on the vibrating portion of vocal folds (Titze 1994). Thus, other conditions being equal, the larger larynx with larger vibration structures should produce a lower fundamental frequency (Fitch and Hauser 2002). However, the rule is

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V. A. Matrosova · I. A. Volodin (✉)
Department of Vertebrate Zoology, Faculty of Biology,
Lomonosov Moscow State University,
Vorobievsky Gory,
Moscow 119992, Russia
e-mail: volodinsvoc@yahoo.com

I. A. Volodin · E. V. Volodina
Scientific Research Department, Moscow Zoo,
B. Gruzinskaya, 1,
Moscow 123242, Russia

A. F. Babitsky
Severtsov Institute of Ecology and Evolution,
Russian Academy of Sciences,
Leninsky prosp., 33,
Moscow 119071, Russia

not universal because larynx grows independently from the rest of body (Fitch and Hauser 1995, 2002). Correlations between body size and call fundamental frequency were not found in a number of species even within same-sex and same-age classes (Lass and Brown 1978; McComb 1991; Collins 2000; Tanaka et al. 2006).

Differences in fundamental frequency according to body size are expected, however, between age classes within a species. As juveniles are always smaller than adult conspecifics, the smaller juvenile larynges with correspondingly shorter vocal folds should produce higher fundamental frequencies (Morton 1977; Owings and Morton 1998). Hypothetically, coincidence of frequencies is possible only in the case of accelerated growth of the juvenile larynx in comparison with other body parts. Data from vocalizations of Carnivores, Primates, and Rodents support these con-

tentions. Table 1 gives examples of maximum fundamental frequencies (f_0 max) for the same juvenile and adult call types. In all but one species (the sea otter, *Enhydra lutris*), where juvenile calls have a lower fundamental frequency than their mothers (McShane et al. 1995), smaller juveniles show higher fundamental frequencies than larger adults.

The ground-dwelling sciurid provide a convenient model for studying individual responses to conspecific alarm calls (e.g., Leger et al. 1979; Hare 1998; Loughry and McDonough 1989; Blumstein and Arnold 1995), including responses to alarms coming from different age classes (Nesterova 1996; Hanson and Coss 2001; Blumstein and Daniel 2004). Few studies, however, provide comparative data on call parameters for different ages (Table 1). For marmots and prairie dogs, the limited available data suggest the usual mammalian pattern, with higher fundamental

Table 1 Reported maximum values (f_0 max, mean \pm SD) and ranges (f_0 range) for the fundamental frequency of juveniles and adults for some Carnivora, Primates, and Rodentia species

| Species | Call type | Juvenile | | | Adult | | Reference |
|------------------------------|-------------------|----------|--------------------------------------|---------------------------|--------------------------------------|------------------|---------------------------|
| | | Age | F_0 max, kHz | F_0 range, kHz | F_0 max, kHz | f_0 range, kHz | |
| Carnivora | | | | | | | |
| <i>Panthera tigris</i> | Meowing | 3–6 m | | 0.2–0.4 | | 0.15–0.2 | Peters 1978 |
| <i>Panthera onca</i> | Meowing | 3–6 m | | 1.0–3.0 | | 0.15–0.4 | Peters 1978 |
| <i>Acinonyx jubatus</i> | Meowing | 1.5–3 m | 3.89 \pm 1.42, $n=38$ | | 1.09 \pm 0.77, $n=60$ | | Volodina 1998, 2000 |
| | Chirping | 1.5–3 m | 5.85 \pm 0.95, $n=142$ | | 1.19 \pm 0.17, $n=33$ | | Volodina 1998, 2000 |
| <i>Lycaon pictus</i> | Hoo-call | 7–8 w | 1.20, $N=6$, $n=63$ | 1.04–1.73, $N=6$, $n=63$ | 0.76, $N=9$, $n=721$ | 0.44–0.88 | Wilden 1997; Hartwig 2005 |
| <i>Enhydra lutris</i> | Scream | 1–4 m | 0.81 \pm 0.05, $N=9$, $n=92$ | | 0.86 \pm 0.12, $N=8$, $n=61$ | | McShane et al. 1995 |
| Primates | | | | | | | |
| <i>Macaca fuscata</i> | Food call, male | 1–3 y | 1.4 \pm 0.6, $N=8$, $n=90$ | | 0.8 \pm 0.3, $N=1$, $n=20$ | | Inoue 1988 |
| | Food call, female | 1–3 y | 1.4 \pm 0.7, $N=4$, $n=40$ | | 0.7 \pm 0.1, $N=15$, $n=127$ | | Inoue 1988 |
| <i>Cebuella pygmaea</i> | Trill | 15–98 w | 13.87, $N=9$ | | 12.48, $N=8$ | | Elowson et al. 1992 |
| Rodentia | | | | | | | |
| <i>Cynomys ludovicianus</i> | Jump-yip | 3–4 m | 1.52, $n=72$ | | 1.31, $n=81$ | | Owings and Loughry 1985 |
| <i>Marmota flaviventris</i> | Alarm call | 1–4 m | 11.2 \pm 1.2 ^a , $N=67$ | | 10.3 \pm 1.0 ^a , $N=29$ | | Blumstein and Munos 2005 |
| <i>Marmota bobac</i> | Alarm call | 3 m | 5.2 | | 3.9 | | Nesterova 1996 |
| | Alarm call | 5 m | 4.56 \pm 0.42, $N=20$, $n=60$ | | 4.06 \pm 0.43, $N=18$, $n=54$ | | Nikol'skii 2007 |
| <i>Spermophilus pygmaeus</i> | Alarm call | 1–2 m | 5.57 \pm 0.41, $N=17$, $n=51$ | | 5.32 \pm 0.41, $N=19$, $n=57$ | | Nikol'skii 2007 |
| <i>Rhombomys opimus</i> | Alarm call | 1–5 m | 2.51 \pm 0.23, $N=17$, $n=51$ | | 2.12 \pm 0.21, $N=17$, $n=51$ | | Nikol'skii 2007 |

Only data on non-ultrasound tonal vocalizations are given.

w Weeks; m months; y years; N number of animals; n number of calls

^a Second harmonic (f_2) was measured.

frequency for juveniles than for adults (Owings and Loughry 1985; Nesterova 1996; Blumstein and Munos 2005; Nikol'skii 2007). For the little ground squirrel *Spermophilus pygmaeus* juveniles, the reported fundamentals of the alarm whistle were also slightly but significantly higher those of adults (Nicol'skii 2007). On the other hand, in the California ground squirrel *S. beecheyi*, spectrograms of whistle alarm calls demonstrate higher fundamentals for adults than for juveniles, in spite of the reported threefold differences in body weight (650–680 g adults vs 210–275 g juveniles; Hanson and Coss 2001). Therefore, unlike marmots and prairie dogs, for ground squirrels, the presence or absence of an age-related shift in the fundamental frequency of the whistle alarm call remains unclear.

The alarm whistle of the speckled ground squirrel (*S. suslicus*) consists of weakly modulated tonal notes about 200 ms in duration with fundamental frequencies ranging from 9–10 kHz (Fig. 1), which are typically produced in series with intervals substantially longer than the duration of the notes themselves (Nicol'skii 1979; Nicol'skii et al. 1984; Volodin 2005). The alarm whistle of the yellow ground squirrel (*S. fulvus*) consists of deeply

modulated tonal notes with maximum fundamental frequency of 5–6 kHz, depth of frequency modulation about 2.5–3 kHz, and note duration about 70 ms (Fig. 1), emitted in clusters of 2–16 notes. These clusters, in their order, may occur singly or be produced repetitively, resulting in series, with intercluster intervals substantially longer than cluster duration (Nicol'skii 1979; Titov et al. 2005).

In this study, we compare fundamental frequencies between age classes for two species of ground squirrels and describe the previously unreported phenomenon of similarity in alarm call frequency between adults and juveniles. In addition, we study relationships between body weight, morphological parameters of the larynx, and alarm whistle fundamental frequencies.

Materials and methods

Subjects and study sites

We recorded alarm whistles from 47 adult and 21 juvenile speckled ground squirrels and from 25 adult and 25

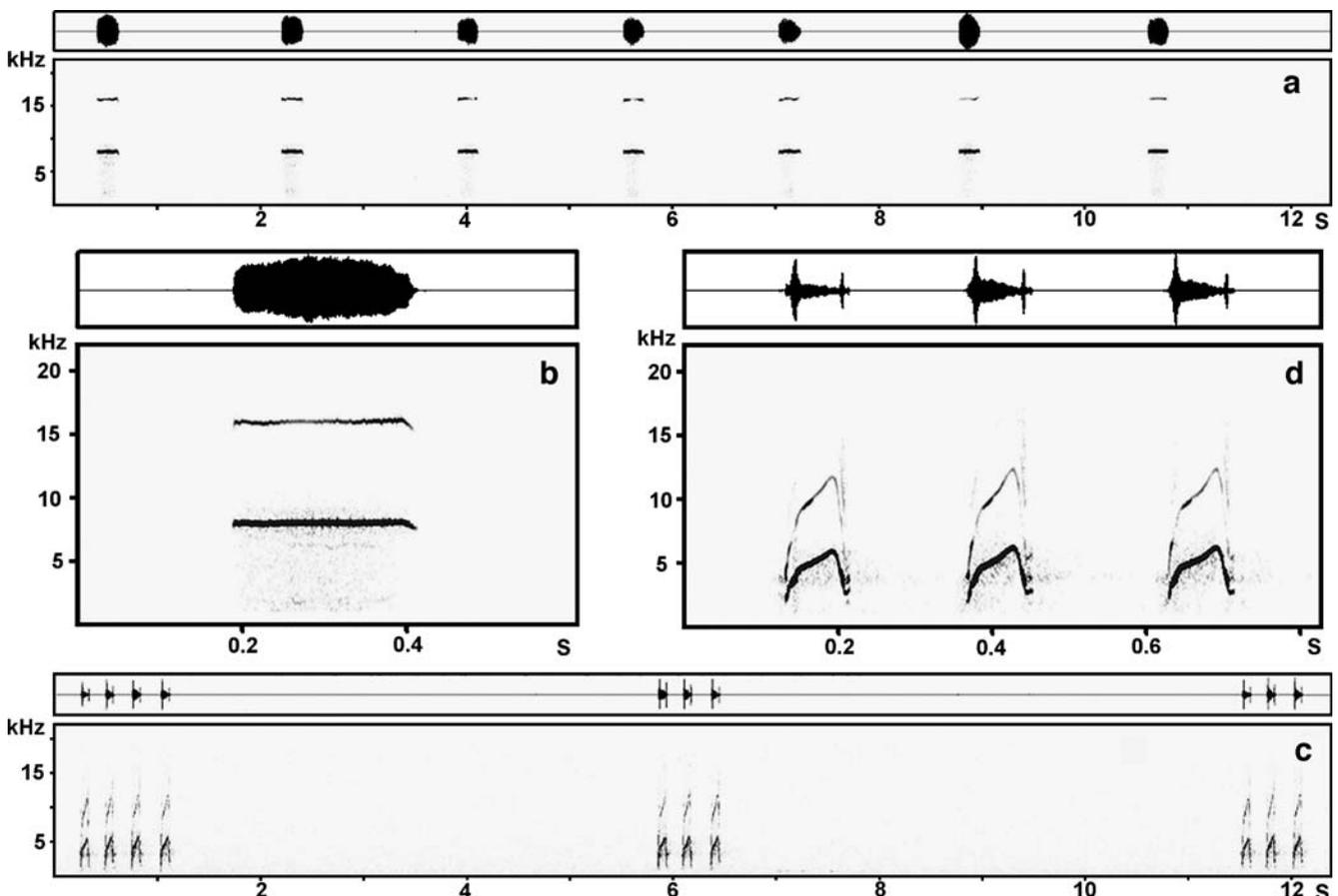


Fig. 1 The whistle alarm calls of the speckled and yellow ground squirrels. **a** Part of a natural series of whistle alarm call notes produced by an individual speckled ground squirrel. **b** Enlarged view of a first

note from the series above. **c** Part of a natural series of whistle alarm call note clusters produced by an individual yellow ground squirrel. **d** Enlarged view of third note cluster from the series below

juvenile yellow ground squirrels in their natural colonies. The speckled ground squirrel colony was located in the Moscow region, Russia (54°47'68"N, 38°42'23"E), and the yellow ground squirrel colony in the Saratov region, Russia (50°43'88"N, 46°46'04"E). Both colonies have been studied since 2001, and all animals are individually marked and repeatedly (once every 2 weeks or more often) captured in live-traps with sunflower seed bait. The "adult" age class included animals 1 year of age and older, while juveniles were pups that emerged from their natal burrows during the year in question. The juvenile speckled ground squirrels emerged from burrows from 24 June to 6 July, 2003 and from 25 June to 4 July, 2004; the juvenile yellow ground squirrels used emerged from 25 May to 9 June, 2005.

Data collection

For the speckled squirrel, we recorded alarm whistles during repetitive 3-day-long visits, occurred once each 2 weeks from 7 May to 31 July, 2003 and from 17 April to 17 July, 2004. For the yellow squirrel, we recorded alarm whistles daily during a period from 29 May through 14 June, 2005. Most juvenile squirrels (20 of 21 speckled and 21 of 25 yellow) were recorded during the first week after their natal emergence, i.e., at the age of 4–5 weeks. The alarm whistles were recorded from squirrels sitting in wire-mesh traps within 1 hour of capture. Animals emitted alarm whistles toward humans spontaneously or in response to additional stimulation (movements of hand-held baseball cap). In live-traps, the pattern of calling toward humans and structure of alarm whistles were similar to the occurred under natural conditions in both the species (Volodin 2005). The similarity between alarm calls produced by free and live-trapped animals was also reported for the California ground squirrel (Hanson and Coss 2001) and for the yellow-bellied marmot (Blumstein and Munos 2005).

On average, recording sessions lasted 4–5 min and provided 30–40 alarm whistle notes per speckled ground squirrel and 20–30 whistle alarm call clusters per yellow ground squirrel. The distance to microphone was about 30 cm for the speckled squirrel and about 100 cm for the yellow squirrel. We used Marantz PMD-222 (D&M Professional, Kanagawa, Japan) cassette recorder with AKG-C1000S (AKG-Acoustics GmbH, Vienna, Austria) cardioid electret condenser microphone and type II chrome audiocassette EMTEC-CS II (EMTEC Consumer Media, Ludwigshafen, Germany). The system provided frequency response 40–14,000 Hz on tape speed 4.75 mm/s.

Call analysis

For both species, we analyzed calls from a single recording session per animal (first session, when more than one

recording session per animal was available). For the speckled ground squirrel, we took measurements from ten randomly selected alarm whistle notes of good quality (not superimposed with wind, noise, or sounds animals make by hitting the live-trap) per animal; however, five animals provided fewer than ten notes. In total, we analyzed 659 alarm whistle notes from 68 speckled squirrels: 463 from 23 adult males and 24 adult females (10 notes per animal from 44 individuals, 9 notes per animal from two individuals, and 5 from one individual), and 196 from 16 juvenile males and 5 juvenile females (10 notes per animal from 19 individuals and 3 per animal from two individuals).

For the yellow ground squirrel, we took measurements from ten alarm whistle notes of good quality per animal, one note per cluster, second in order within a cluster. In total, we analyzed 500 alarm whistle notes from 50 yellow squirrels: 250 from 12 adult males and 13 adult females (10 notes per animal) and 250 from 12 juvenile males and 13 juvenile females (10 notes per animal).

All call analyses were made with Avisoft SASLab Pro software v. 4.33 (Avisoft Bioacoustics, Berlin, Germany). Calls were digitized with 44,100 Hz sampling frequency and 16-bit precision. Spectrograms were created using Hamming window, FFT-length 512 points, frame 50%, and overlap 87.5%. These settings provided a bandwidth of 224 Hz, frequency resolution of 86 Hz, and time resolution of 1.45 ms.

In the speckled squirrel, the alarm whistle notes were weakly modulated in frequency, so it was difficult to determine a position of f_0 max visually (Fig. 2). In these calls, the fundamental frequency band coincided with frequency of maximum amplitude (f peak). So we used the "automatic parameter measurements" option of Avisoft SASLab Pro to extract the fundamental frequency values. After high-pass filtration at 1,000 Hz to remove background noise, we automatically measured f_0 for each of 21 single power spectra, taken with equal intervals from beginning to end of a call note. Then, the f_0 max of a call note was automatically selected from these 21 point values.

In the yellow squirrel, the alarm whistle notes were deeply modulated in frequency, so the f_0 max was clearly visible (Fig. 2). Thus, for this species we measured f_0 max of a call note directly from the screen with the reticule cursor.

For both species, f peak was taken automatically from the mean power spectrum over the entire call note (Fig. 2). In the speckled squirrel, the fundamental frequency always was the highest energy band. Similarly, in the yellow squirrel, the fundamental frequency had the highest energy relative to the harmonics. Thus, in both the species, f peak was located within a fundamental frequency band. All measurements of f_0 max and f peak were exported automatically to Microsoft Excel (Microsoft, Redmond, WA, USA).

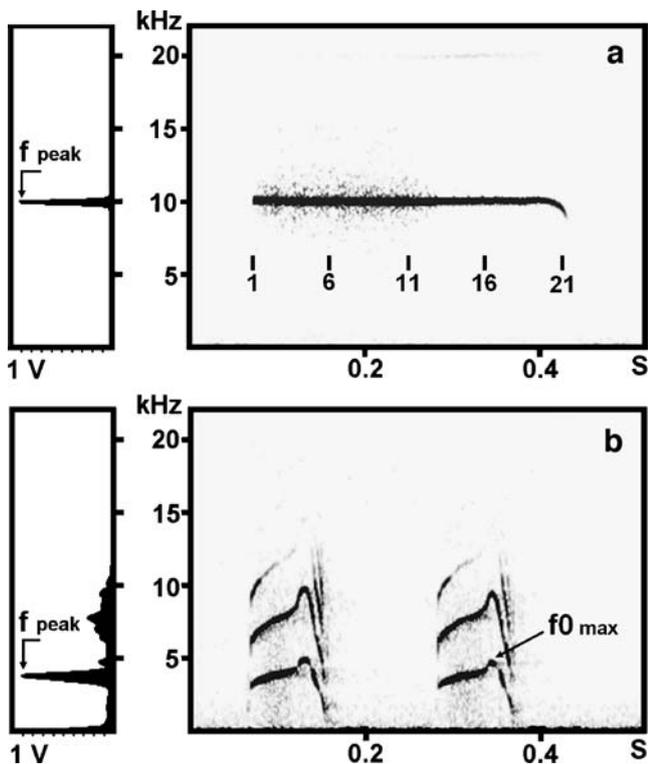


Fig. 2 Whistle alarm call parameters. **a** Measurements taken from alarm whistle notes of the speckled ground squirrel: *left* frequency of maximum amplitude (f peak) measures, taken from the mean power spectrum over the entire call note; *right* maximum fundamental frequency (f_0 max) measures, selected as maximum of 21 measures taken throughout a call note. The scale numbers below the call note show 1, 6, 11, 16, and 21 points of measures. **b** Measurements taken from alarm whistle notes (second note within each cluster) of the yellow ground squirrel: *left* frequency of maximum amplitude (f peak) measures, taken from the mean power spectrum over the entire call note; *right* point of measurement of the maximum fundamental frequency (f_0 max)

Body weight and skull measurements

All body weight measurements (one per animal) were made on electronic scales (Tefal Ovelys 79881 Groupe SEB, Ecully Cedex, France) with 1-g precision after a recording session from the same animals that provided calls for analysis. However, for the speckled ground squirrel, weight data were not obtained for one adult female and one juvenile male, so weight data were available only for 46 adult and 20 juvenile squirrels. For the yellow ground squirrel, body weight data were recorded for all adults and juveniles.

To approximate linear sizes of adult and juvenile squirrels, we also measured skulls of 60 speckled squirrels (34 adults and 26 juveniles) and 65 yellow squirrels (34 adults and 31 juveniles) from the collection of the Zoological Museum of Moscow State University (ZM MSU), representing multiple collection sites within the range of the species. We measured the condylobasale skull length from the most prominent point of praemaxillare (between incisors) to the distal end of condylus occipitalis

with vernier calipers HC-200 (Kalibr, Moscow, Russia) with 0.05-mm precision.

Larynx measurements

We excised larynges of one adult and one juvenile of each species that died of diseases or a car accident. After fixation with ethanol, the larynges were peeled from the surrounding soft tissues and photographed with a Canon A95 (Canon, Tokyo, Japan) digital camera together with calibration scale, from both the ventral and lateral views. Morphological measurements of a larynx and trachea were made from both lateral and ventral photo images using Scion Image (Scion, Frederick, MD, USA) software with 0.05-mm precision (Fig. 3).

We measured the width of the thyroid cartilage on the ventral view at its narrowest place approximately in the middle of its height and on the lateral view—from prominence of the dorsal part to the middle of the lateral edge. The height of the thyroid cartilage was measured as the length of its frontal edge. The larynx height was measured from the depression in the dorsal part of the thyroid cartilage to the caudal edge of the dorsal part of the cricoid cartilage. The tracheal diameter was measured from ventral view between the first and second cartilage ring caudal to the larynx (Fig. 3).

Statistical analyses

We applied the nonparametric Mann–Whitney U test for all comparisons between samples and the Spearman rank order correlation to estimate the relations between the body weights and mean values of the alarm whistle parameters. All statistical analyses were made in Statistica, v. 6.0 (StatSoft, Tulsa, OK, USA), and differences were considered significant where $p < 0.05$.

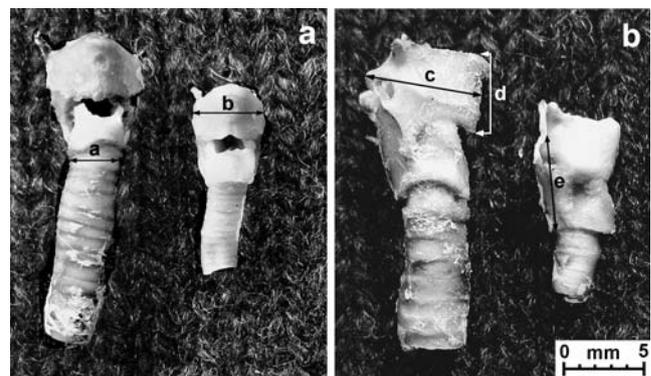


Fig. 3 **a** Ventral view of adult (*left*) and juvenile (*right*) larynges of the speckled ground squirrel. **b** Lateral view of adult (*left*) and juvenile (*right*) larynges of the yellow ground squirrel. Morphological measurements: *a* tracheal diameter; *b* width of the thyroid cartilage taken from ventral view; *c* width of the thyroid cartilage taken from lateral view; *d* height of the thyroid cartilage; *e* laryngeal height

Table 2 Mean (\pm SD; minimum–maximum) values for the maximum fundamental frequency (f_0 max) and frequency of maximum amplitude (f peak) for the measured whistle alarm call notes, body weight, and skull length of adult and juvenile speckled and yellow ground squirrels

| Call parameter | Speckled squirrel | | | Yellow squirrel | | |
|-------------------|-----------------------------|-----------------------------|-------------|----------------------------|----------------------------|-------------|
| | Juvenile | Adult | Ratio j/a | Juvenile | Adult | Ratio j/a |
| f_0 max (kHz) | 9.73 \pm 0.63; 8.43–11.71 | 9.66 \pm 0.75; 6.42–11.80 | 1.01 | 5.41 \pm 0.52; 4.13–6.72 | 5.52 \pm 0.42; 4.57–6.46 | 0.98 |
| f peak (kHz) | 9.50 \pm 0.73; 8.34–11.54 | 9.49 \pm 0.69; 6.32–11.45 | 1.00 | 4.05 \pm 0.62; 3.10–6.02 | 4.16 \pm 0.81; 2.67–5.77 | 0.97 |
| Body weight (g) | 89 \pm 34; 49–170 | 222 \pm 50; 134–368 | 0.40 | 187 \pm 72; 90–495 | 1091 \pm 274; 407–1485 | 0.17 |
| Skull length (mm) | 34.6 \pm 3.0; 27.9–38.5 | 39.3 \pm 2.4; 33.2–43.2 | 0.88 | 46.0 \pm 4.0; 36.8–54.7 | 57.2 \pm 3.5; 49.0–64.5 | 0.80 |

Ratio j/a shows ratio of juvenile-to-adult mean values.

Results

Table 2 shows f_0 max and f peak for alarm whistle notes, and body weight and skull length for adults and juveniles of the two species. In the speckled ground squirrel, both f_0 max and f peak values did not differ significantly between the ages ($U=43006$, $p=0.29$ and $U=44406$, $p=0.66$, respectively). Moreover, in the yellow ground squirrel, the f_0 max was significantly higher in adults than in juveniles ($U=26317$, $p<0.01$), whereas the f peak did not differ significantly between the ages ($U=29421$, $p=0.26$).

However, both the body weight and the skull sizes were significantly larger in adults in the speckled ground squirrel ($U=8$, $p<0.001$ and $U=95$, $p<0.001$, respectively) and in the yellow ground squirrel ($U=1$, $p<0.001$ and $U=17$, $p<0.001$ respectively). Further, in juvenile speckled squirrels, the mean body weight value was only 40% of adult body weight, whereas the mean body weight value of juvenile yellow squirrels was as little as 17% of adult body weight (Table 2).

For each species, we did not find significant correlations between the individual mean frequencies (f_0 max and f_0 peak) and body weight, either within the age classes or for pooled samples of all animals within species (Fig. 4). Moreover, all correlation coefficients were very low, varying between 0.01 and 0.33 in absolute values (Table 3).

In both species, juvenile larynges were smaller in all morphological measurements than those of adults (Table 4). The ratios of juvenile-to-adult values in the morphological measurements of larynges were comparable with ratios calculated for skull length values, for both species (Table 2).

Discussion

In the two species examined, the body weight, skull length values, and larynges were significantly smaller in juveniles than in adults. These differences, however, did not correspond to shifts in call frequencies that normally accompany growth of the larynx and vocal tract with

development. Neither f_0 max nor f peak of the alarm whistle differed between the juvenile and adult speckled squirrels, and in the yellow squirrel, f_0 max was significantly lower in juveniles than adults. In this paper, we discuss the lack of acoustical cues to body size in the two ground squirrel species and propose a functional explanation for the absence of any difference in frequency between juveniles and adults.

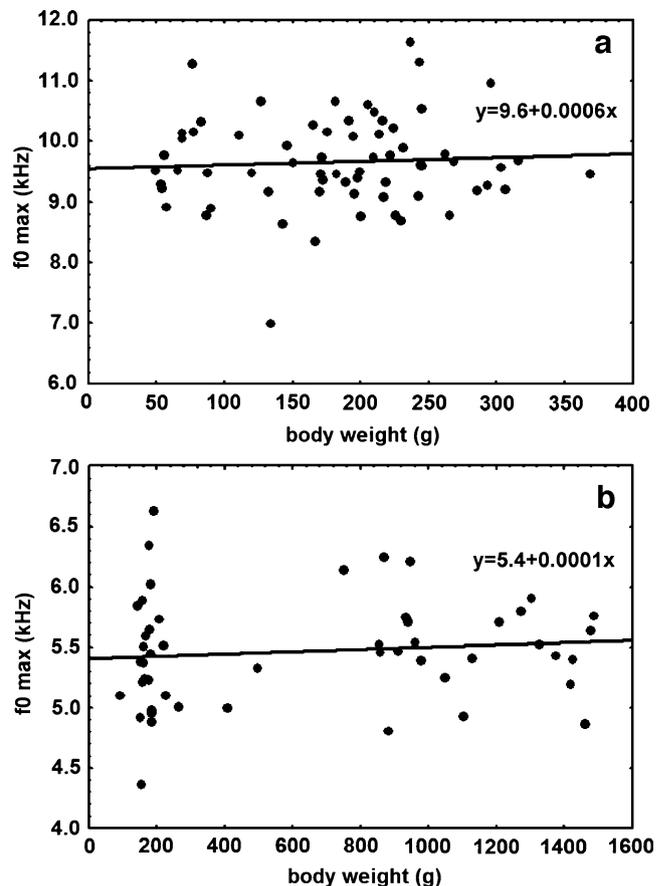


Fig. 4 The relationship between body weight and maximum fundamental frequency (f_0 max) in the whistle alarm call of the speckled (a) and yellow (b) ground squirrels for pooled samples of adults and juveniles

Table 3 Spearman rank correlation coefficients (r_s) between body weight (BW) and individual mean values of fundamental frequency parameters

| Species | Age classes | Correlation between | r_s | p level |
|-------------------|------------------|---------------------|-------|-----------|
| Speckled squirrel | Adult (46) | BW and f_0 max | 0.11 | 0.46 |
| | | BW and f peak | 0.10 | 0.51 |
| | Juvenile (20) | BW and f_0 max | 0.04 | 0.86 |
| | | BW and f peak | 0.16 | 0.51 |
| | All animals (66) | BW and f_0 max | 0.04 | 0.74 |
| Yellow squirrel | Adult (25) | BW and f peak | 0.09 | 0.50 |
| | | BW and f_0 max | -0.10 | 0.62 |
| | Juvenile (25) | BW and f peak | -0.01 | 0.96 |
| | | BW and f_0 max | 0.01 | 0.98 |
| | All animals (50) | BW and f peak | -0.33 | 0.11 |
| | | BW and f_0 max | 0.13 | 0.37 |
| | | BW and f peak | 0.03 | 0.85 |

f_0 max Maximum fundamental frequency, f peak frequency of maximum amplitude; number of animals in parentheses

Acoustical cues to body size in the two ground squirrel species

The formant cues to body size can be revealed in the call structure only under conditions of comparatively uniform distribution of sound energy over a call spectrum, otherwise the vocal tract resonances cannot be extracted (Owren and Rendall 1997). In the alarm whistle of our two ground squirrel species, the sound energy was concentrated within the fundamental frequency and widely spaced harmonics. In the speckled ground squirrel, the alarm whistle was practically non-modulated, and nearly all energy was concentrated within a narrow fundamental frequency band. This structure resulted in very small differences between the values of maximum fundamental frequency and frequency of maximum amplitude. In the yellow ground squirrel, the alarm whistle was much more strongly modulated; however, there was only a single power peak at the level of a short plateau of fundamental frequency, just below its maximum. Therefore, in both species the sound source was the main determinant of the energy distribution in the alarm whistle spectrum, and the derived energy spectra did not allow the formant structure to become apparent. Therefore, in spite of the well-expressed and significant differences between juveniles

and adults in skull size and body weight, the alarm whistles of these species did not provide formant cues to body size.

We expected that cues to body size would be apparent in the fundamental frequency of the alarm whistle. However, the source-based vocal cues to size were also absent in these species. At the same time, we found, that juvenile larynges were smaller than those of adults in both species, with laryngeal differences proportionate to those found for skull measurements. Thus, growth of the juvenile larynx was not accelerated relative to other body parts. Nevertheless, this did not prevent juvenile speckled squirrels from producing calls with the same, and juvenile yellow squirrels—even lower fundamental frequencies, than adult conspecifics. In addition, we did not find correlations between the fundamental frequency of alarm whistles and body weight within age classes of the two species (Table 3).

We therefore propose that these species may actively manipulate elements of their vocal apparatus, adjusting the alarm whistle fundamental frequency (by varying the length of vibrating portion of vocal folds, the degree of their stretching, subglottal pressure level, etc.). Such manipulation would allow squirrels to sever the relationship between larynx size and call frequency; however, physiological research is necessary to test this hypothesis. For humans,

Table 4 Morphological measurements (mm) of juvenile and adult larynges for the speckled and yellow ground squirrels made from lateral and ventral views of photo images

| Larynx measurements | Speckled squirrel | | | Yellow squirrel | | |
|--|-------------------|-------|-------------|-----------------|-------|-------------|
| | Juvenile | Adult | Ratio j/a | Juvenile | Adult | Ratio j/a |
| Width of the thyroid cartilage, ventral view | 4.45 | 6.00 | 0.74 | 5.55 | 6.65 | 0.83 |
| Width of the thyroid cartilage, lateral view | 4.45 | 4.90 | 0.91 | 4.95 | 7.25 | 0.68 |
| Height of the thyroid cartilage | 3.15 | 3.75 | 0.84 | 3.70 | 4.80 | 0.77 |
| Laryngeal height | 5.15 | 6.45 | 0.80 | 6.30 | 8.55 | 0.74 |
| Tracheal diameter | 2.40 | 3.00 | 0.80 | 2.95 | 4.45 | 0.66 |

Ratio j/a shows ratio of juvenile-to-adult values.

the ability to vary the vowel frequency during singing, for example, with transition to falsetto, has been reported (Fitch and Hauser 1995). Another example comes from observations of vocal development in crane chicks (Gruidae): from hatching to 8–9 months, a crane chick retains its juvenile high call frequency, in spite of the fact that its size and body weight increase enormously (Niemeier 1979; Gebauer and Kaiser 1998).

The similarity in frequencies between age classes within species may be more widespread than previously supposed. As reported earlier, juvenile sea otter vocalizations have lower fundamental frequencies than those of adults (Table 1). More extensive data are necessary to determine whether the phenomenon proposed is widespread among mammals.

Indistinguishable fundamental frequencies: possible adaptive significance

In both species, adults and juveniles produce alarm whistles with similar fundamental frequencies. In this study, we consider three relevant hypotheses and argue, which of those is most consistent with our data.

Hypothesis of optimal sound transmission through environment The apparent consistency in call structure across age classes can readily be explained by selection favoring optimal transmission characteristics of the alarm call in a cooperative society (reviewed by Blumstein 2007). In this case, however, alarm call characteristics should be confined to a relatively narrow frequency range, optimal for propagation through the environment. Instead, in the two ground squirrel species being examined, we observed widely varying ranges for f_0 max and f peak values between individuals of any age class (Table 2). That is, both the adult and juvenile call sets envelope sounds, widely varying in their propagation characteristics, but nearly entirely overlapping between the age classes. Therefore, our data do not support this hypothesis.

Hypothesis of ecologically relevant space (active space) The high-frequency alarm calls are propagated over a shorter distance in comparison with more low frequency, so they can be heard only by closest neighbors (Wilson and Hare 2006; Blumstein 2007). In accordance with this hypothesis, adults can increase their alarm call frequency to make the alarm calls less detectable to predators. Reduction of active space is only adaptive if the distance between neighboring ground squirrels is shorter than predator detection distance. In speckled ground squirrels, there were no differences in average call frequencies in different years, despite the twofold difference in population density in the study years (Babitsky et al. 2006). As distance between animals is

inversely related to density, this observation is not consistent with the active space hypothesis.

It should also be noted that the hypothesis is mostly relevant for consideration of alarm calls that differ dramatically in frequency, and therefore, propagation range within species, such as ultrasound and audible alarm calls in the Richardson's ground squirrel *Spermophilus richardsonii* (Wilson and Hare 2006). For the audible alarm calls of the two ground squirrel species examined, the overall ranges of variability in fundamental frequency within species did not exceed a few kilohertz, both in adults and in juveniles (Table 2). Therefore, even the highest and the lowest frequencies should not differ strongly in their active space. In this case, to reduce the active space, transfer to ultrasound alarm seems much more reasonable. As audible alarm calls are very similar between the Richardson's ground squirrel and the speckled ground squirrel (Sloan et al. 2005), it may only be a matter of time before ultrasonic calls are described for speckled ground squirrels as well. At least some of the animals produced in live-traps not only ordinary alarm calls but also 'whisper calls' (as described by Wilson and Hare 2004) characteristic of ultrasonic vocalizations in Richardson's ground squirrels.

Hypothesis of vocal mimicry In this study, we advance a hypothesis that indistinguishable fundamental frequencies between age classes represent some kind of vocal mimicry. It is impossible to decide whether the juveniles mimic adults, or vice versa. However, we can hardly imagine any functional explanation for the latter. In addition, from an anatomical viewpoint, juvenile larynges are more elastic and their cartilages are more flexible. Therefore, it seems that juveniles can more easily manipulate the length of their vocal folds.

At the same time, it is possible that natural selection favors vocal mimicry in juvenile ground squirrels, i.e., they lower the pitch of their alarm whistles to pretend they are adult and thus avoid age-dependent risk. There are two conditions necessary for vocal mimicry to be effective. First, alarm calls have to come from the dense vegetation or other kinds of shelters, so that the actual size of the vocalizing animal cannot be seen. Invisibility of a caller is a necessary condition for the development of the "vocal size exaggeration," which evolved independently in a few taxa of birds and mammals (Fitch 1999; Fitch and Hauser 2002). Both the speckled and yellow ground squirrels regularly emit alarm whistles from burrows with only head protruding above the soil surface or from dense vegetation, which grows high at the study sites by the time of natal emergence. Some species of marmots have also been shown to produce alarm calls from burrows (Nikol'skii

and Vinogradov 2000). Second, vocal mimicry is only adaptive if the juveniles are more likely to be preyed upon than adult animals. There are no quantitative studies on predation in these two species so far. But for both of them, there are predators, dangerous for juveniles, but not for adults: the steppe polecat *Mustela eversmanni* and the marbled polecat *Vormela peregusna*, in the case of the yellow ground squirrel (Ismagilov 1969), and the weasel *M. nivalis*, in the case of the speckled ground squirrel (Lobkov 1999). These predators hunt in burrows, they do not eat adult ground squirrels, and they cause significant juvenile mortality. In 2001, in our study site, one steppe polecat terminated a whole litter of five juvenile yellow squirrels in 1 day (Tchabovsky, unpublished data). With such rates of predation even a small advantage due to vocal mimicry could be of considerable value.

One peculiar type of predator, namely conspecifics, deserves separate discussion, as juvenile ground squirrels may suffer from infanticide more than from interspecific predators (Hanson and Coss 2001). Infanticide is extremely widespread among Marmotinae (Sherman 1981; Ebensperger 1998). Although infanticide is usually hard to detect (Hrdy 1979; Hoogland 1995) and most of Marmotinae were not subjects for long-term field studies, at least 15 species (more than 20% of the subfamily) have been shown to be infanticidal (Ebensperger and Blumstein 2007). Infanticide may be even more widespread in the subfamily than is currently known. Infanticide has been reported in the yellow ground squirrel in the wild (Ismagilov 1952, 1969). The speckled ground squirrel, although not yet shown to commit infanticide in the wild, demonstrated infanticidal behavior in captivity (Lobkov 1999). As speckled ground squirrels are also opportunistic cannibals (Lobkov 1999), the discovery of infanticide in this species may be a matter of time.

The phenomenology of infanticide differs among ground squirrel species. Infanticide can be committed by either females (Waterman 1984; Hare 1991; Hoogland 1995; Trulio 1996), males (McLean 1983), or both (Sherman 1981). Killers can either eat their victims (Sherman 1981; Hoogland 1995; Trulio 1996) or leave them (Sherman 1981; McLean 1983). Killers can be neighbors of the victims and attack when the mother is absent, relying on visual information. As ground squirrel's alarm calls are individually distinguishable (Hare 1998; McCowan and Hooper 2002; Volodin 2005), it may be practically impossible to deceive neighboring animals by means of vocal mimicry. On the other hand, the vocal mimicry can reduce the probability of being killed by a conspecific hunting for juveniles it does not know individually. Thus, vocal mimicry may be an adaptation to 'resource exploitation' but not 'resource competition' based infanticide (Hrdy 1979; Ebensperger 1998; Ebensperger and Blumstein 2007).

Of course, ground squirrels can also use other vocal cues to assess age besides the fundamental frequency (Hanson and Coss 2001), but even the elimination of a single cue to age may convey some selective advantage. Our hypothesis could be directly tested by playing back alarm calls to small mustelids, which are a threat to juvenile but not adult ground squirrels. The prediction is that these mustelids will preferentially be attracted to calls of higher frequency.

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