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AN UNUSUAL EFFECT OF MATURATION ON THE ALARM CALL FUNDAMENTAL FREQUENCY IN TWO SPECIES OF GROUND SQUIRRELS

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ABSTRACT

In most mammals, adults produce relatively low frequency vocalizations compared to those of juveniles. This rule is not maintained however at least in four species of ground squirrels, whose juveniles call at the adult's fundamental frequency. These findings have been obtained however with separate sets of juveniles and adults and no data is available concerning the ontogeny linked to these differences. Here we analyze the acoustic structure of alarm calls of the same Yellow *Spermophilus fulvus* and Speckled *S. suslicus* ground squirrel individuals, recorded as pups and as adults after hibernation. We found the fundamental frequencies of adults within the same frequency ranges as those of pups, in spite of the significant difference in body mass. In ground squirrels, severing the relationship between body size and call frequency removes some vocal cues to age. We discuss some functional hypotheses advanced to explain manipulations with fundamental frequencies in ground squirrels and other animals, and suggest the lack of data for discussing the mechanisms of such vocal tuning.

Keywords: maturation, anti-predatory behaviour, vocalization, alarm call, rodent, *Spermophilus*, ground squirrel

INTRODUCTION

In most mammals, the larger body size of adults correlates with their relatively low frequency sound production to those of their conspecific juveniles (Morton 1977). This is because the larger larynges and larger vocal tracts commonly produce lower calls. This rule is not maintained however at least in four species of *Spermophilus* ground squirrels. In juvenile Speckled Ground Squirrels *S. suslicus* and Richardson's Ground Squirrels *S. richardsonii,* fundamental frequencies are restricted within the same range of values as in adults (Matrosova *et al.* 2007; Swan & Hare 2008), whereas in juvenile California Ground Squirrels *S. beecheyi* and Yellow Ground Squirrels *S. fulvus*, fundamental frequencies are even lower than in adults (Hanson & Coss 2001; Matrosova *et al.* 2007).

Similar fundamental frequencies between juvenile and adult ground squirrels mean that this aspect of sound production can not convey cues about body size differences, as it occurs in most mammalian vocalizations (Fitch & Hauser 2002). Sound is produced by the larynx (sound source) with air flow that comes from the lungs and then passes through air cavities of vocal tract (sound filter), including the pharynx, oral and nasal cavities. Therefore, three acoustic modalities reflect body size in mammals: the duration of a call that relates to lung capacity, the fundamental frequency of a call that reflects the size of larynx, and the formant frequencies reflecting the dimensions of vocal tract (Fant 1960; Titze 1994; Fitch & Hauser 2002). With their larger lungs, larynges and vocal tracts, adults generally should produce calls of longer duration, lower fundamental frequency and with lower formants than their conspecific juvenile counterparts (Morton 1977; Owings & Morton 1998; review: Matrosova *et al.* 2007).

As formants are well-expressed only in wideband sounds (Fitch 1999; Owren & Rendall 2001; Fitch & Hauser 2002), the tonal narrowband alarm calls of Yellow and Speckled ground squirrels lack also the filter-related cues to body size. Each of the two species emits a single type of alarm call toward multiple predators, either terrestrial or aerial. Alarm calls of Speckled Ground Squirrels are single long notes, whereas those of Yellow Ground Squirrels are clusters of a few short notes (Figures 1, 2).

We can suggest that differences in lung capacity between juveniles and adults likely should result in the production of shorter calls by juveniles (Fitch & Hauser 2002). Also, it remains unclear how fundamental frequencies change with maturation during individual life histories of the Yellow and Speckled ground squirrels. The previous data suggesting no differences in fundamental frequencies of alarm calls with ages were obtained from independent samples of juvenile and adult individuals (Matrosova *et al.* 2007). A repeated measures design with the same subjects at different ages is needed to confirm these unusual findings. Distinct from the cross-sectional approach, where individuals are grouped into age classes (e.g. Lee *et al.* 1999), the repeated measures approach (e.g. Hollien *et al.* 1994) allows to follow individual trends in voice shifts with age. The purpose of this study was to examine the age-dependent shifts in duration and fundamental frequency of alarm calls recorded from the same individual Yellow and Speckled ground squirrels twice, as 4-7 weeks old juveniles, and as yearlings.

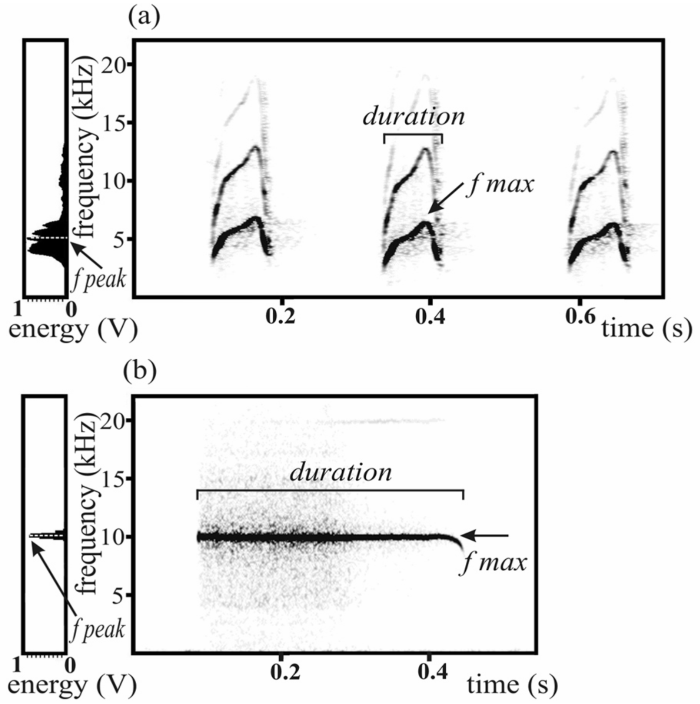

Figure 1. Measurements taken from alarm call notes: (a) – second alarm call note within a cluster of the Yellow Ground Squirrel; (b) – alarm call note of the Speckled Ground Squirrel. f0 max – the maximum fundamental frequency, f peak – the maximum amplitude frequency, duration – the duration of the alarm call notes.

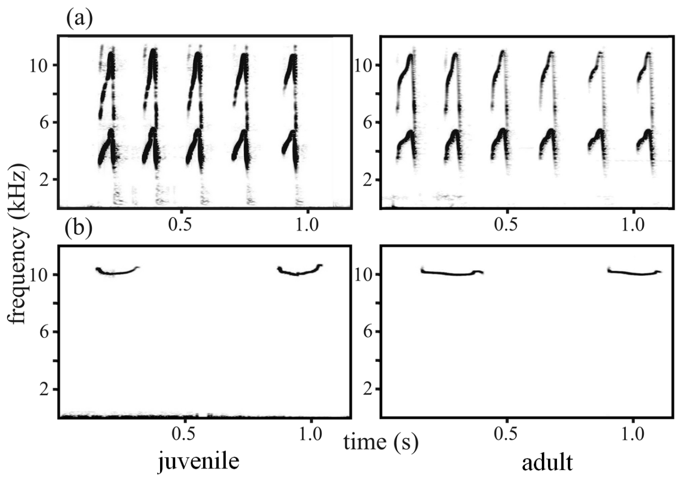

Figure 2. Spectrograms of alarm calls, recorded from the same individual, first as a juvenile (left), then as an adult (right): (a) – Yellow Ground Squirrels, (b) – Speckled Ground Squirrels.

MATERIALS AND METHODS

Subjects and study site

We recorded alarm calls and measured body mass of 8 (3 male, 5 female) Yellow Ground Squirrels and of 7 (1 male, 6 female) Speckled Ground Squirrels during brief capture-recaptures occurring between 08.00 and 20.00 hours in their natural colonies in Saratov province, Russia (50°43′88″ N, 46°46′04″ E; 31.6 hectares) and in Moscow province, Russia (54º47’68” N, 38º42’23” E; 28 hectares) respectively. Each individual was recorded once between mid-May and mid-June through two successive years, i.e., in 2005-2006, or 2006-2007. During the first year an animal was recorded as a juvenile of 4-7 weeks of age and in the second year as an adult. We considered overwintered animals as adults, because yearlings of both species can breed after their first hibernation (Babitsky *et al.* 2006; Popov *et al.* 2006), that lasts between eight to nine months in each species (Ismagilov 1969; Shekarova *et al.* 2003). Time between any such two recordings averaged 347 ± 32 days for Yellow Ground Squirrels and 340 ± 18 days for Speckled Ground Squirrels.

For capturing Yellow Ground Squirrels, 3 to 5 loops and 2 to 3 wire-mesh live traps of original construction 80 × 80 × 80 cm without bait, per 10-hectare study grid, were applied. In this live trap, the top is missing, and it has a falling door in the bottom. For capturing, the live trap is placed onto the entrance of a burrow from above and the door is opened and set so that it falls when an animal emerges from its burrow. For acoustic recording, each Yellow Ground Squirrel was placed singly into a 30 × 15 × 15-cm wire-mesh hutch. For capturing and subsequent recording Speckled Ground Squirrels, 20-23 wire-mesh live-traps, 30 × 10 × 10 cm, with sunflower seed bait, per 2-hectare study grid, were applied.

Call recording procedure and equipment

All acoustic recordings were made within one hour of capture from individually marked animals. From the live trap or hutch, animals emitted calls toward a human observer, sitting within 2 m, either spontaneously or in response to additional stimulation (movements of hand-held baseball cap). The distance to microphone was about 30 cm for Speckled squirrels and about 100 cm for Yellow squirrels. The difference in microphone distance between species was due to the differences in relative loudness of their calls. On average, a recording session lasted 3-4 min and provided 20-40 alarm calls per animal. We used a 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). After recording, animals were weighed with 1 g precision and released back at the place of capture. Study colonies, dates of above ground activity and hibernation, capture protocols, method of marking with dye and chips and weighting procedures are described in detail in Matrosova *et al*. (2007, 2009, 2010).

Acoustic analyses

Digitisation (44.1 kHz, 16 bit precision), creation of spectrograms (Hamming window, FFT 512 points, frame 50%, overlap 87.5%) and measurements were conducted using Avisoft SASlab Pro software v. 4.33 (Avisoft Bioacoustics, Berlin, Germany). We analyzed up to 10 randomly selected alarm calls, not overlapped with a noise, per recording per animal. In total, we analyzed 145 alarm calls for Yellow Ground Squirrels (76 for juveniles and 69 for adults) and 136 alarm calls for Speckled Ground Squirrels (68 for juveniles and 68 for adults). Parameters selected for analysis of voice changes with maturation were the maximum fundamental frequency (*f0 max*), maximum amplitude frequency (*f peak*) and duration of alarm call notes (Figure 1).

In Speckled Ground Squirrels, alarm call notes were weakly modulated in frequency, so it was difficult to determine a position of *f0 max* visually. In these calls, the fundamental frequency band was the band of maximum intensity. So we used the "automatic parameter measurements" option of Avisoft SASLab Pro to extract the *f0* values. After high-pass filtration at 1 kHz to remove background noise, we automatically measured the *f0* for each of 21 single power spectra, taken with equal intervals from beginning to end of a call note. Then, the *f0 max* of a call was automatically selected from these 21 point values. In the Yellow Ground Squirrel, the alarm call notes within clusters were deeply modulated in frequency, so the *f0 max* was clearly visible. Thus for this species we measured *f0 max* of a second call note in a cluster from the screen with the reticule cursor. For both the species, *f peak* was taken automatically from the mean power spectrum over the entire call note. In both the species, the *f peak* was located within fundamental frequency band. Call durations were measured with the standard marker cursor in the spectrogram window. All measurements were exported automatically to Microsoft Excel (Microsoft, Redmond, WA, USA).

Statistical analyses

We applied parametric tests, as a Kolmogorov-Smirnov test showed that distributions of parameter values did not depart from normality ($p > 0.05$). We used a one-way repeated measures ANOVA to test the influence of age on the individual mean parameter values for calls of first year and second year recordings and on the body mass measures of first year and second year in each species. Also, we used a two-way repeated measures ANOVA with age entered as the repeated measure and species as a fixed factor to compare the age effects on call parameters and body mass between species. The statistical analyses were made with STATISTICA, v. 6.0 (StatSoft, Inc., Tulsa, OK, USA), all means are given as mean ± SD and differences were considered significant whenever $p < 0.05$.

RESULTS

Both examined species showed indistinguishable *f0 max* and *f peak* frequencies between juvenile and adult age groups (Figure 2, Table 1). Individual trends for the maximum fundamental frequency values showed that the *f0 max* decreased with age in 4 of 8 Yellow and in 2 of 7 Speckled Ground Squirrels and increased with age in the rest 8 of 15 study animals (Figure 3). In the Yellow Ground Squirrel, the

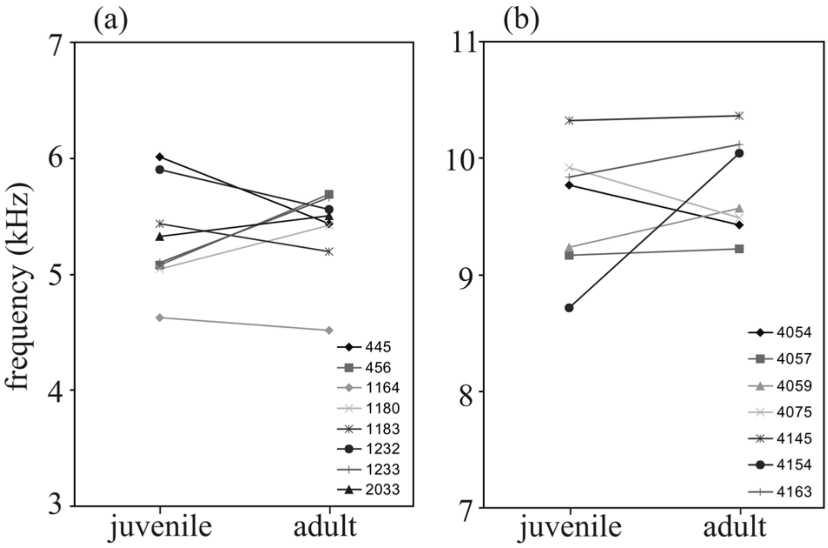

Figure 3. Alarm call notes maximum fundamental frequencies showed different trends with age between individuals: (a) – Yellow Ground Squirrels, (b) – Speckled Ground Squirrels. Numbers are individual numbers of animals.

TABLE 1

Values (mean ± SD; minimum – maximum) for the alarm call note parameters and for body mass of juvenile and adult Yellow and Speckled ground squirrels and results of comparison with repeated measures ANOVA. *f0 max* – the maximum fundamental frequency, *f peak* – the maximum amplitude frequency, *duration* – the duration of the alarm call notes. Significant *p*-values are given in bold.

Parameter	Yellow Ground Squirrel (n=8)			Speckled ground Squirrel (n=7)		
	juvenile	adult	ANOVA results	juvenile	adult	ANOVA results
f0 max (kHz)	5.32±0.46; 4.63–6.01	5.37±0.38; 4.52–5.69	$F_{1,7}$=0.14, p=0.72	9.86±0.62; 9.11–10.78	9.96±0.52; 9.47–10.75	$F_{1,6}$=0.17, p=0.69
f peak (kHz)	4.20±0.70; 3.58–5.76	4.44±0.84; 3.68–5.54	$F_{1,7}$=0.40 p=0.55	9.57±0.55 8.72–10.32	9.75±0.42 9.22–10.37	$F_{1.6}$=0.67, p=0.44
Duration (ms)	68±9; 54–79	63±8; 53–75	$F_{1,7}$=0.90, p=0.37	218±23; 184–260	273±67; 190–380	$F_{1,6}$=6.47, **p=0.04**
Body mass (g)	283±120; 173–555	819±430; 307–1428	$F_{1,7}$14.62, **p=0.007**	98±33; 58–148	205±59; 106–300	$F_{1,6}$=27.94, **p=0.002**

differences in duration between ages were non-significant. In Speckled Ground Squirrels, the duration of alarm call notes was significantly shorter in juveniles than in adults (Table 1). At the same time, during the year-long maturation period passed between the two recording sessions, body mass increased significantly in both the species (Table 1).

The between-species comparison for the age effects with two-way repeated measures ANOVA showed non-significant differences in the developmental trends of the *f0 max* and *f peak* ($F_{1,13}$ = 0.02, p = 0.90 for both comparisons). On the other hand, the developmental trends of the duration differed significantly between species ($F_{1,13}$ = 8.2, p = 0.013), as in the Speckled Ground Squirrel the duration of alarm call notes showed increase with age, whilst in the Yellow Ground Squirrel it retained unchanged. As body mass increase was stronger in Yellow Ground Squirrels compared to Speckled ones (2.9 and 2.1 times respectively, Table 1), the developmental trends of body mass differed significantly between species ($F_{1,13}$ = 8.0, p = 0.014).

DISCUSSION

While the usual trends of voice change with maturation in mammals show lower fundamental frequency in adults compared to pups (Matrosova *et al.* 2007), here we documented the irregular shifts in the fundamental frequency with maturation in two ground squirrels. As a result, juveniles and adults of both species produced alarm calls within the same ranges of fundamental frequencies, in spite of large differences in body mass between ages. Thus, this study, with the same animals recorded as pups and adults, confirmed the previous findings that the cues to body size, based on the fundamental frequency, are absent both in Yellow and Speckled ground squirrels (Matrosova *et al.* 2007).

The developmental trends of the *f0 max* and *f peak* were the same in both species, in spite of their prominent differences in body size, ecology and sociality. At the same time, the developmental trends of body mass reflected prominent differences in body size between species. Both species are diurnal, herbivorous, obligatory-hibernating sciurids (Lobkov 1999; Efimov 2005). However, the Yellow Ground Squirrel is the largest-sized *Spermophilus* ground squirrel, inhabiting rather open habitats (Efimov 2005; Tchabovsky 2005; Vasilieva *et al.* 2009; Matrosova *et al.* 2010), and able to form the matrilinear population structure (Matrosova *et al.* 2008). Sociality in the Yellow Ground Squirrel is evident from the male hierarchy during the mating period (Bokshtein *et al.* 1989), from the social play that occurs between littermates, and from the affiliative mother-offspring contacts, occurring up to hibernation (Vasilieva & Tchabovsky 2009). In contrast, the Speckled Ground Squirrel is less social compared to the Yellow one, does not form matrilineas, is small-sized compared to other ground squirrels and inhabits rather closed habitats with high grass cover (Lobkov 1999; Tchabovsky 2005; Matrosova *et al.* 2009).

In the Speckled Ground Squirrel, the alarm call note duration was significantly shorter in juveniles relative those of adults. However, in the Yellow Ground Squirrel, the differences in duration of the second note in a cluster were non-significant between ages. Thus, the cues to body size based on temporal parameters of alarm calls were presented only in the Speckled Ground Squirrel. Single call notes of Speckled Ground Squirrels are comparable with within-cluster notes of Yellow Ground Squirrels, because a Yellow Ground Squirrel makes an extra inspiration before each note within cluster (our unpublished data). Therefore, in both species each alarm call note represents a vocal emission during a single expiration. However, while Speckled Ground Squirrels probable use all their lung capacity to produce each alarm call note, Yellow Ground Squirrels do not use it exhaustively. We can propose it because Speckled Ground Squirrels produce longer calls compared to those of Yellow Ground Squirrels, which are much larger than Speckled Ground Squirrels in their sizes. Nevertheless, in the Richardson's Ground Squirrel, which is larger than the Speckled Ground Squirrel, but produces alarm calls of very similar acoustic structure, no significant age-related differences in the alarm call duration has been found (Swan & Hare 2008).

To separate the physical relationships between fundamental frequency values and body size, both species of ground squirrels probably tune their vocal characteristics. The tunings of fundamental frequencies have also been reported for nonsciurid mammals and birds. Rocky Mountain Elks *Cervus elaphus nelsoni* produce their rut calls of 1 kHz fundamental frequency with their 3 cm long vocal folds, while predicted fundamental frequencies are 50 Hz (Riede & Titze 2008). Among birds, Red-Crowned Cranes *Grus japonensis* support their juvenile high fundamental frequency of 2-4 kHz throughout their adolescence up to 8-9 months, in spite of the 48 times increase of their body mass, probably to provoke a prolonged parental care toward offspring with infantile vocal characteristics (Klenova *et al.* 2009, 2010). The manipulations with fundamental frequencies should be impossible if vocal characteristics followed the vocal anatomy by default (Fitch & Hauser 2002).

It is most plausible that juveniles tuned their vocal characteristics to match those of adults. From an anatomical viewpoint, juvenile larynges are more elastic and they can more easily manipulate the length of their vocal folds. From a functional viewpoint, juvenile ground squirrels mimicking adults could reduce the risks associated with predation and intra-specific aggression (Matrosova *et al.* 2007). Besides the fundamental frequency, ground squirrels can use also other vocal cues to age (Hanson & Coss 2001), and the findings of this study suggest that the alarm call duration may provide such a cue in the Speckled Ground Squirrel. But under heavy selection for vocal mimicry, even the elimination of a single cue to age may convey some selective advantage. Juvenile sciurids are predated much more often compared to adults (Sibly *et al.* 1997). Mammalian predators, which hunt ground squirrels above ground, can be deceived when vegetation is dense in June and July, during and after the emergence of juvenile Yellow and Speckled ground squirrels from their natal burrows.

The Steppe Polecat *Mustela eversmanni* and the Marbled Polecat *Vormela peregusna* are major predators of juvenile Yellow squirrels (Ismagilov 1969), and the Weasel *M. nivalis* is the major predator of juvenile Speckled squirrels (Lobkov 1999). These mustelidae are too small to predate adult ground squirrels and they could considerably influence juvenile mortality. In our study grids, in 2001 one steppe polecat predated a whole litter of five juvenile Yellow squirrels in one day, and in 2007 six different individual weasels were captured into live traps for Speckled Ground Squirrels within three days during a period of juvenile emergence from their natal burrows (our unpublished data). Also, juvenile ground squirrels may suffer from infanticide even more than from interspecific predators (Hanson & Coss 2001). Among marmotinae, at least 12 species were shown to be infanticidal (Ebensperger 1998; Ebensperger & Blumstein 2007). Also, infanticide was found in wild Yellow Ground Squirrels (Ismagilov 1969) and captive Speckled Ground Squirrels (Lobkov 1999). Adult animals never suffer from infanticide, so infanticide may be another factor responsible for the vocal mimicry in ground squirrels. Results of playback research with Richardson's Ground Squirrels provide a strong support for the hypothesis of vocal mimicry (Swan & Hare 2008). In this species, lacking both the fundamental frequency-based and duration-based cues to age, adults do not recognize between alarms of adult and juvenile conspecifics.

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