

The potential to encode sex, age, and individual identity in the alarm calls of three species of Marmotinae

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Abstract In addition to encoding referential information and information about the sender's motivation, mammalian alarm calls may encode information about other attributes of the sender, providing the potential for recognition among kin, mates, and neighbors. Here, we examined 96 speckled ground squirrels (*Spermophilus suslicus*), 100 yellow ground squirrels (*Spermophilus fulvus*) and 85 yellow-bellied marmots (*Marmota flaviventris*) to determine whether their alarm calls differed between species in their ability to encode information about the caller's sex, age, and identity. Alarm calls were elicited by approaching individually identified animals in live-traps. We assume this experimental design modeled a naturally occurring predatory event, when receivers should acquire information

about attributes of a caller from a single bout of alarm calls. In each species, variation that allows identification of the caller's identity was greater than variation allowing identification of age or sex. We discuss these results in relation to each species' biology and sociality.

Keywords *Marmota flaviventris* · *Spermophilus fulvus* · *Spermophilus suslicus* · Alarm call · Acoustic communication · Antipredator behavior

Introduction

While mammalian and avian alarm calls function to reduce predation risk to the caller or conspecifics, there is additional acoustic variation that may provide information about the caller's attributes (Rendall et al. 2009). In many mammals, vocalizations encode information about the caller's sex, age, or identity (e.g., Leger et al. 1984; Cheney and Seyfarth 1990; Durbin 1998; Frommolt et al. 2003; Torriani et al. 2006). Within-species variation of acoustic signals provides a potential for recognition among kin, mates, and neighbors. Between-species variation may be related to species-specific social structures.

Among ground-dwelling sciurid rodents, alarm calls are the most prominent acoustic signal. Besides their primary functions of warning conspecifics of predators (Sherman 1977; Blumstein 2007), or informing predators that they have been detected (Woodland et al. 1980; Sherman 1985; Hasson 1991; Shelley and Blumstein 2005; Digweed and Rendall 2009a, b), alarm calls of ground-dwelling sciurids may provide concomitant information about the caller's sex, age, and identity. Individual-specific alarm calls were reported for steppe marmots *Marmota bobak* (Nikol'skii and Suchanova 1994), Belding's ground squirrels *Spermo-*

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philus beldingi (Leger et al. 1984; McCowan and Hooper 2002), yellow-bellied marmots *Marmota flaviventris* (Blumstein and Munos 2005), speckled ground squirrels *Spermophilus suslicus* (Volodin 2005; Matrosova et al. 2009), yellow ground squirrels *Spermophilus fulvus* (Matrosova et al. 2010a, b), European ground squirrels *Spermophilus citellus*, and Taurus ground squirrels *Spermophilus taurensis* (Schneiderová and Policht 2010). In Richardson's ground squirrels *Spermophilus richardsonii* (Hare 1998) and yellow-bellied marmots (Blumstein and Daniel 2004), playbacks demonstrated the ability to distinguish among calls of familiar and unfamiliar individuals.

Sex differences were found in alarm calls of yellow-bellied marmots (Blumstein and Munos 2005), but not in speckled ground squirrels (Volodin 2005). Age-related features were found in alarm calls of black-tailed prairie dogs *Cynomys ludovicianus* (Owings and Loughry 1985), steppe marmots (Nesterova 1996; Nikol'skii 2007), yellow-bellied marmots (Blumstein and Munos 2005), little ground squirrels *Spermophilus pygmaeus* (Nikol'skii 2007), and speckled ground squirrels (Volodina et al. 2010), but not in Richardson's ground squirrels (Swan and Hare 2008) or yellow ground squirrels (Volodina et al. 2010). Consistently, playback studies revealed distinctive responses to alarm calls of adults and pups in California ground squirrels *Spermophilus beecheyi* (Hanson and Coss 2001), yellow-bellied marmots (Blumstein and Daniel 2004) and steppe marmots (Nesterova 1996), but not in Richardson's ground squirrels (Swan and Hare 2008).

Thus, ground-dwelling sciurids represent a convenient group for determining what kinds of acoustic parameters—frequency, temporal, or amplitude (or combinations of them)—are responsible for encoding and decoding specific information (e.g., a caller's identity, sex, or age). Furthermore, by examining to which extent alarm calls differ between individuals, the sexes, and age classes among different species of Marmotinae, we can determine the relative importance of these cues for different species in relation to their biology and sociality.

To date, the relative contribution of different acoustic variables to the discrimination of age, sex, and identity has been studied in detail only for a single species, the yellow-bellied marmot (Blumstein and Munos 2005). The current study expands on this study to focus on interspecific variation in ratios of age, sex, and individual variability of the yellow-bellied marmot and of two species of *Spermophilus* ground squirrels, where the first species, *S. fulvus*, is of comparable size and sociality as yellow-bellied marmots (Tchabovsky 2005; Matrosova et al. 2010a), and the second one, *S. suslicus*, is much smaller and less social than both species (Tchabovsky 2005; Matrosova et al. 2009).

S. fulvus is the largest ground squirrel. It inhabits open steppe and desert habitats with patchy grasses. Individuals place their burrows on local topographic features (Kashkarov

and Lein 1927; Ismagilov 1969) which permits group members to monitor each other. This visibility may favor its relatively advanced sociality compared to the smaller *Spermophilus* species (Tchabovsky 2005). Sociality they are characterized by having: (1) a male hierarchy during the mating period (Bokshtein et al. 1989); (2) social play that occurs between littermates, and (3) affiliative mother–offspring contacts from emergence to their first hibernation (Vasilieva et al. 2009). Like marmots (Armitage 1999), many female *S. fulvus* hold the same home territories for years, and this results in stable local groups based on female kinship (Shilova et al. 2006; Matrosova et al. 2008; Vasilieva et al. 2009). While *M. flaviventris* are among the least-social species of marmots (Armitage 1991), *S. fulvus* and *M. flaviventris* are similarly social in that females form groups based on kinship and young disperse at yearlings, rather than as juveniles.

By contrast, *S. suslicus* do not form groups based on female kinship, pups disperse as juveniles, and the species is relatively small compared with other ground squirrels (Tchabovsky 2005). They live in relatively closed habitats, covered with high grasses that block visibility during much of their active season (Volodin et al. 2008).

We hypothesized that alarm calls of more social species should provide more cues about caller identity because there is a greater need for individual discrimination within social groups in more social species. Also, we expected more cues about age and sex in the more social species, as these are features related to different social roles in sciurids (Blumstein and Armitage 1997). The purpose of this study was to identify acoustic correlates of the caller's identity, sex, and age in these three sciurid species and to examine the relationships between these acoustic cues and features of social organization.

Materials and methods

Subjects and study sites

We recorded alarm calls from three species. Our subjects were 52 adult and 44 juvenile *S. suslicus*, 50 adult and 50 juvenile *S. fulvus* and 38 adult and 47 juvenile *M. flaviventris*. *S. suslicus* were recorded in the Moscow region, Russia (54°47'68"N, 38°42'23"E), *S. fulvus* in the Saratov region, Russia (50°43'88"N, 46°46'04"E), and *M. flaviventris* were recorded in the Upper East River Valley, Gunnison County, Colorado, USA (38°57'N, 106°69'W). Marmots at this Colorado site have been studied continuously since 1962 (Armitage 1991); both ground squirrel colonies have been studied since 2001. All animals were individually marked and repeatedly captured in live-traps. Detailed methods of animal trapping and marking can be

found in Armitage (1982), Blumstein and Munos (2005) for the marmots, and Matrosova et al. (2007, 2009, 2010a) for ground squirrels. For this study, the “adult” age class included animals that were in their second season of life, and “juveniles” were pups that emerged from their natal burrows during the year of data collection.

Data collection

We recorded alarm calls of *M. flaviventris* from June–August 2001–2003. *S. suslicus* were recorded from May–June 2003–2006. *S. fulvus* were recorded from May–June 2005–2008. The recordings were made during the season of pup raising in all the species. Alarm calls were recorded from individually marked animals of known age and sex sitting in wire-mesh traps, within 1 h of capture. Marmot alarm calls were recorded 20–40 cm from calling subjects; *S. suslicus* calls were recorded about 30 cm; and *S. fulvus* calls were recorded about 100 cm from calling subjects. This variation in the distance to microphone among species was related to differences in relative call loudness and was sufficiently far to avoid near-field effects. Animals emitted alarm calls toward humans spontaneously or in response to additional stimulation (movements of hand-held hats). Calls elicited in live-traps in response to humans are similar to naturally elicited alarm calls (Blumstein and Munos 2005; Matrosova et al. 2007, 2010b). Subjects were weighed after recording their calls (1 g precision for squirrels and 25 g precision for marmots).

Calls were recorded using either a Marantz PMD-222 analog tape recorder with an AKG-C1000S cardioid electret condenser microphone (frequency response, 40 Hz–14 kHz), a CF-recorder Marantz PMD-671 with a Sennheiser K6 ME-64 cardioid electret condenser microphone

(frequency response, 40 Hz–24 kHz, sampling rate 48.0 kHz), with digital audio tape decks Sony PCM-M1 or Tascam DA-P1 (sampling rate 44.1 kHz) and Audix OM-3xb microphones (frequency response, 40 Hz–20 kHz). The frequency response curves of all microphones were flat over the whole range of the spectra of the alarm calls recorded, thus the use of different types of recording equipment did not confound our acoustic measurements. For data transferring and further acoustic analyses, we used a MOTU 828 Firewire external digital board (Mark of the Unicorn, Cambridge, MA, USA) with a Macintosh PowerBook G4 (Apple computer, Cupertino, CA, USA) and Canary 1.2.4 (Charif et al. 1995), Sound-Edit 16 (Macromedia 1995), and Avisoft SASLab Pro v. 4.3 (Avisoft Bioacoustics, Berlin, Germany) software. For both *Spermophilus* species, calls were digitized at 24 kHz sampling frequency and 16-bit precision and high-pass filtered at 1 kHz to remove background noise. For *M. flaviventris*, calls were digitized at 44.1 kHz sampling frequency and 16-bit precision and not filtered. For all species, spectrograms for analysis were created using Hamming window, Fast Fourier transform length 1,024 points, frame 50%, and overlap 96.87%.

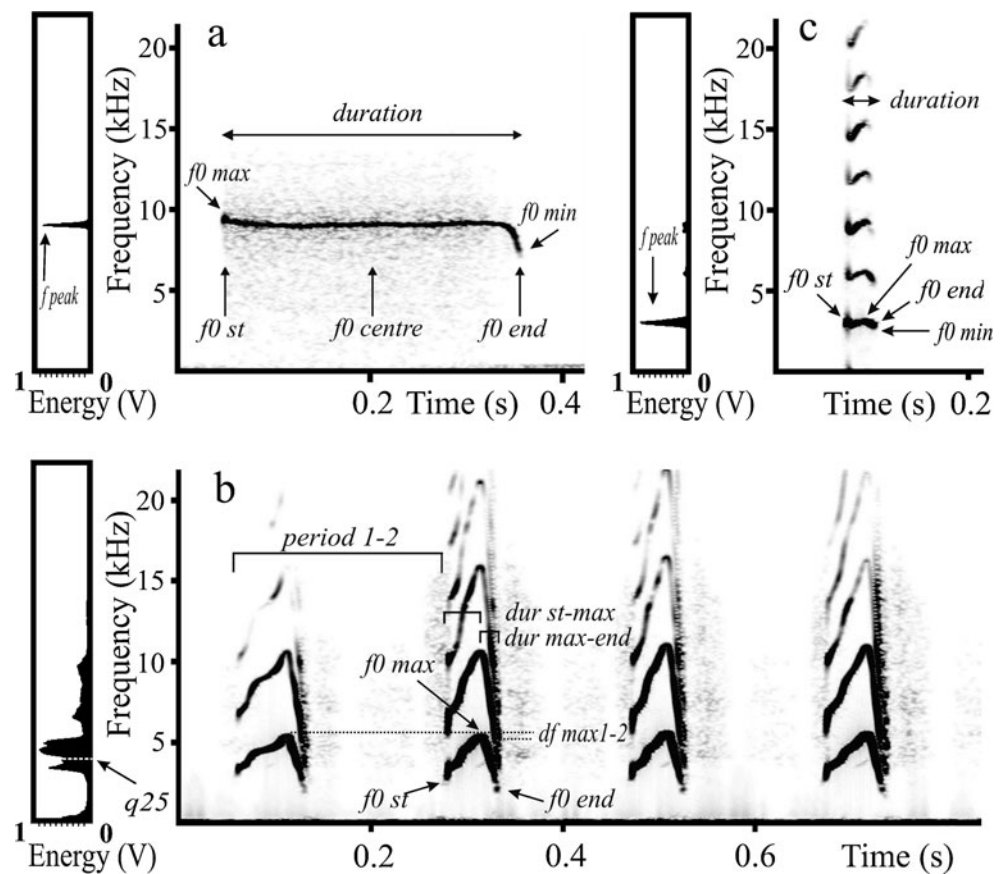
Call analysis

For all species, we analyzed calls from a single recording session per animal (first session, when more than one recording session per animal was available). We took measurements (Table 1) from ten randomly selected alarm call notes of good quality (not superimposed with wind or noise) per ground squirrel and from alarm call notes per marmot (12 animals provided fewer notes; four *S. suslicus* provided seven to eight notes, seven *S. fulvus* provided six

Table 1 Variables of alarm calls of three species of Marmotinae: speckled ground squirrel *S. suslicus*, yellow ground squirrel *S. fulvus*, and yellow-bellied marmot *M. flaviventris*

Variable	Description	Species
<i>f0 max</i>	The maximum fundamental frequency of a note (kHz)	All
<i>f0 st</i>	The fundamental frequency at the start of a note (kHz)	All
<i>f0 end</i>	The fundamental frequency at the end of a note (kHz)	All
<i>f0 min</i>	The minimum fundamental frequency of a note (kHz)	<i>S. suslicus</i> , <i>M. flaviventris</i>
<i>f0 centre</i>	The fundamental frequency in the middle of a note (kHz)	<i>S. suslicus</i>
<i>f peak</i>	The maximum amplitude frequency of a note (kHz)	<i>S. suslicus</i> , <i>M. flaviventris</i>
<i>q25</i>	The value of the first energy quartile of a second note in a cluster (kHz)	<i>S. fulvus</i>
<i>bnd</i>	The width of maximum amplitude frequency band at −20 dB (kHz)	<i>S. suslicus</i> , <i>M. flaviventris</i>
<i>duration</i>	Total duration of a note (ms)	<i>S. suslicus</i> , <i>M. flaviventris</i>
<i>dur st-max</i>	The time period from the beginning to the point of maximum fundamental frequency of a note (ms)	<i>S. fulvus</i>
<i>dur max-end</i>	The time period from the point of maximum fundamental frequency to the end of a note (ms)	<i>S. fulvus</i>
<i>d ampl</i>	The difference between the amplitudes of fundamental frequency and first harmonic bands (dB)	<i>M. flaviventris</i>
<i>period 1-2</i>	The time period from the start of a first note to the start of a second note in a cluster (ms)	<i>S. fulvus</i>
<i>df max 1-2</i>	The difference between the maximum fundamental frequencies of a first and of a second note in a cluster (kHz)	<i>S. fulvus</i>

Fig. 1 Spectrograms and mean power spectra illustrating the measured variables in three species of Marmotinae: **a** speckled ground squirrels *S. suslicus*; **b** yellow ground squirrels *S. fulvus*; and **c** yellow-bellied marmots *M. flaviventris*. For designations see Table 1



to nine notes, one *M. flaviventris* provided four notes). In total, we analyzed 949 alarm calls from 96 *S. suslicus* (514 from adults, 435 from juveniles), 984 alarm calls from 100 *S. fulvus* (497 from adults, 487 from juveniles), and 424 alarm calls from 85 *M. flaviventris* (190 from adults, 234 from juveniles).

In *S. suslicus* and *M. flaviventris*, alarm calls are single notes, weakly modulated in frequency, so it was difficult to determine a position of f_0 maximum visually (Fig. 1). We used the “automatic parameter measurements” option of Avisoft SASLab Pro or waveforms in Canary to extract the fundamental frequency values (f_0 max, f_0 st, f_0 max, f_0 end,

f_0 centre) and duration of each alarm call note (see Blumstein and Munos 2005 and Matrosova et al. 2007, 2009 for measurement details). From the mean power spectrum, we measured the f_{peak} of a call note, d_{ampl} and bnd (see Table 1 for description of all variables).

S. fulvus alarm calls represent clusters of two to 16 notes, deeply modulated in frequency, so the f_0 max was clearly visible and had the highest energy relative to the harmonics (Fig. 1). Thus, for this species we measured f_0 max, f_0 st, f_0 max, and f_0 end (Table 1) of a note directly from the screen with the reticule cursor (see Matrosova et al. 2007, 2010a, b for measurement details). Since many clusters consisted of

Table 2 GLMM results for effects of factors “sex”, “age”, and “identity” on the alarm call variables in speckled ground squirrels *S. suslicus*

Variable	Factor		
	Sex	Age	Identity
Duration	$F_{1,853}=1.38$; $p=0.24$	$F_{1,853}=5.27^*$	$F_{93,853}=38.19^{***}$
f_0 st	$F_{1,853}=0.002$; $p=0.97$	$F_{1,853}=0.75$; $p=0.39$	$F_{93,853}=149.41^{***}$
f_0 centre	$F_{1,853}=0.13$; $p=0.72$	$F_{1,853}=0.60$; $p=0.44$	$F_{93,853}=176.23^{***}$
f_0 end	$F_{1,853}=0.28$; $p=0.60$	$F_{1,853}=3.13$; $p=0.08$	$F_{93,853}=64.96^{***}$
f_0 max	$F_{1,853}=0.11$; $p=0.75$	$F_{1,853}=2.54$; $p=0.11$	$F_{93,853}=232.01^{***}$
f_0 min	$F_{1,853}=0.16$; $p=0.69$	$F_{1,853}=0.62$; $p=0.43$	$F_{93,853}=59.89^{***}$
f_{peak}	$F_{1,853}=0.10$; $p=0.76$	$F_{1,853}=0.64$; $p=0.43$	$F_{93,853}=170.85^{***}$
bnd	$F_{1,853}=0.01$; $p=0.93$	$F_{1,853}=9.39^{**}$	$F_{93,853}=10.62^{***}$

F -ratios of GLMM.

Significant effects are given in bold

* $p < 0.05$, ** $p < 0.01$,

*** $p < 0.001$

only two notes, and the first note in a cluster was often more variable than subsequent notes, we fully measured the second note. From mean power spectra, we automatically measured q_{25} . We calculated *dur st-max* and *dur max-end* (Table 1). Also, for each cluster, we measured *period 1-2* and calculated *df max 1-2* (Table 1).

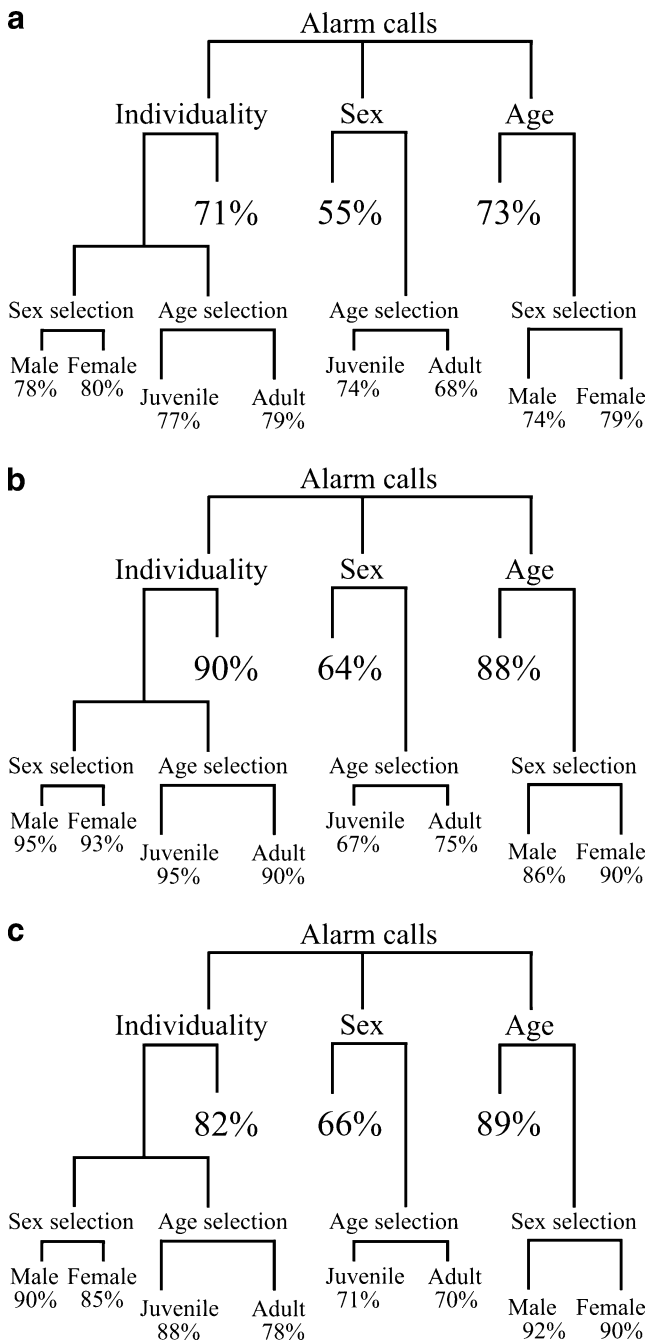


Fig. 2 Schematic representation for DFA values of correct assignment of alarm calls to individual, sex, and age: **a** speckled ground squirrels *S. suslicus*, $N=96$ animals; **b** yellow ground squirrels *S. fulvus*, $N=100$ animals; **c** yellow-bellied marmots *M. flaviventris*, $N=85$ animals

For each species, we measured eight acoustic variables (Fig. 1, Table 1) and used two rules to select variables. First, we wished to minimize the correlation among variables, and second, we wished to maximize the potential for discrimination among individuals. For *S. suslicus* and *S. fulvus*, we selected the eight variables that were the least correlated of (respectively) 31 and 18 variables on the basis of principal component analyses. For these species, these variables also had the largest F -values in ANOVA on individual identity (Matrosova et al. 2010a). For *M. flaviventris*, we selected eight variables that were useful for individual discrimination (Blumstein and Munos 2005). By selecting variables to maximize individual discrimination, we could potentially enhance the individual discrimination compared with sex and age discrimination. However, this effect should be equal for all the three study species and is in no way confounding.

Statistics

All statistical analyses were conducted using STATISTICA, v. 6.0 (StatSoft, Tulsa, OK, USA). All tests were two-tailed, and differences were considered significant whenever $p < 0.05$. We used parametric tests, after determining that parameter values approximated normal distributions (Kolmogorov–Smirnov test, $p > 0.05$). To estimate the effects of factors “sex”, “age”, and “identity” on the alarm call structure, we fitted General Linear Mixed Models (GLMM), with “sex” and “age” as fixed factors and “identity” as a random factor. Identity was preliminarily nested into the factors “sex” and “age”. This statistical design allowed us to estimate the effect of identity without effects of sex and age of a particular individual. Using discriminant function analysis (DFA), we calculated the values of correct assignment of alarm calls to individual, sex, or age. In each DFA, we used all eight measured variables per species and estimated the relative importance of these variables for discrimination using Wilks’ lambda values. We used χ^2 test to compare the obtained values of correct assignment to individual or sex–age group.

To validate DFA results, we calculated the random values of correct assignment to individual, sex, and age for each species using randomization procedure with 300 permutations (Solow 1990) with macros, created for STATISTICA. Using a distribution obtained by the permutation, we noted whether the observed value exceeded 95% or 99% of the values within the distribution (Solow 1990; Matrosova et al. 2010a, b).

We used DFA results to compare the degree of individual-, sex-, and age-related characteristics in the alarm calls of three species because DFA results depend primarily on the number of groups (individuals in the current analyses) analyzed and on the number of variables

on which the classification is based (Hurlburt 2003). In the current study, samples of individuals were large (to provide the high inter-group variability) and nearly equal (85, 96, and 100 individuals), and the number of acoustic variables included into DFA (Table 1) were equal.

Results

Speckled ground squirrels (*S. suslicus*)

Table 2 presents GLMM results for effects of factors “sex”, “age”, and “identity” on the alarm call variables in the *S. suslicus*. We found strong effects of caller identity on all alarm call parameters. The effects of age were significant only for two parameters, and no effects of sex were found (Table 2).

A DFA classifying alarm calls to sex correctly assigned 54.8% of the calls (Fig. 2a) that did not significantly exceed the random value (53.6%). A separate DFA for adults correctly assigned 67.9% to sex, and a separate DFA for pups correctly assigned 74.5% to sex. In order of decreasing importance, the *f0 st*, *duration*, *bnd*, and *f0 max* were mainly responsible for discrimination.

A DFA classifying alarm calls to age correctly assigned 73.1% to age (Fig. 2a) that significantly exceeded ($p < 0.01$) the random value (54.9%). A separate DFA for males correctly assigned 74.0% to age, and a separate DFA for females correctly assigned 79.1% to age. In order of decreasing importance, the *duration*, *f0 max*, *f0 end*, and *f0 min* were mainly responsible for discrimination.

A DFA classifying alarm calls to individual correctly assigned 71.2% of the calls (Fig. 2a) that did significantly exceed ($p < 0.01$) the random value (5.7%). A separate DFA for adults correctly assigned 79.2% to individual; a separate DFA for pups correctly assigned 77.5% to individual; a separate DFA for males correctly assigned 77.9% to

individual, and a separate DFA for females correctly assigned 79.5% to individual. In order of decreasing importance, the *duration*, *f0 end*, *f0 st*, and *bnd* were mainly responsible for discrimination.

Therefore, in *S. suslicus*, assignment to sex did not differ from the random value; assignment to age was 1.5 times the random value, and assignment to individual was 12 times the random value. Figure 2a summarizes the DFA results for within-species variation of alarm calls in *S. suslicus*. Moreover, some parameters that were the most important ones for age or sex discrimination were also the most important ones for individual discrimination. The *duration* was among variables of most importance in all three DFAs. This suggests that sex- and age-related variation in call structure was based on the same acoustic cues, and these were also used for individual-level discrimination. Table 3 presents descriptive statistics for alarm call variables included into DFA and body weight for two age classes and two sex/gender classes of the *S. suslicus*.

Yellow ground squirrels (*S. fulvus*)

Table 4 presents GLMM results for effects of factors “sex”, “age”, and “identity” on alarm call variability in *S. fulvus*. We found significant effects of identity on all variables. We found significant effects of age on seven of the eight variables; however, only three of these effects were comparable to the effects of identity. Effects of sex were significant for three of the eight variables, but these effects were much weaker than effects of age and especially caller identity.

A DFA classifying alarm calls to sex correctly assigned 64.3% (Fig. 2b), exceeding significantly ($p < 0.01$) the random value (53.6%). A separate DFA for adults correctly assigned 75.1%, and a separate DFA for pups correctly assigned 66.9%. In order of decreasing importance, the

Table 3 Values (means±SD) for the alarm call variables and body mass for age–sex classes of speckled ground squirrels *S. suslicus*

Variable	Males		Females	
	Adults <i>N</i> =26 animals <i>n</i> =257 calls	Juveniles <i>N</i> =23 animals <i>n</i> =228 calls	Adults <i>N</i> =26 animals <i>n</i> =257 calls	Juveniles <i>N</i> =21 animals <i>n</i> =207 calls
<i>duration</i> (ms)	235±61	222±48	256±60	220±47
<i>f0 st</i> (kHz)	9.64±0.56	9.36±0.53	9.25±0.88	9.79±0.49
<i>f0 centre</i> (kHz)	9.55±0.51	9.26±0.50	9.21±0.79	9.72±0.47
<i>f0 end</i> (kHz)	9.41±0.65	9.16±0.77	9.00±0.84	9.80±0.62
<i>f0 max</i> (kHz)	9.74±0.55	9.57±0.54	9.41±0.80	10.02±0.54
<i>f0 min</i> (kHz)	9.32±0.59	8.94±0.65	8.91±0.85	9.53±0.50
<i>f peak</i> (kHz)	9.57±0.53	9.27±0.48	9.22±0.78	9.74±0.46
<i>bnd</i> (kHz)	0.44±0.16	0.49±0.22	0.41±0.13	0.52±0.21
<i>mass</i> (g)	215±34	88±37	205±30	74±21

Table 4 GLMM results for effects of factors “sex”, “age”, and “identity” on the alarm call variables in yellow ground squirrels *S. fulvus*

Variable	Factor		
	Sex	Age	Identity
<i>dur st-max</i>	$F_{1,884}=1.20$; $p=0.28$	$F_{1,884}=6.02^*$	$F_{97,884}=76.79^{***}$
<i>dur max-end</i>	$F_{1,884}=1.45$; $p=0.23$	$F_{1,884}=36.75^{***}$	$F_{97,884}=38.23^{***}$
<i>f0 st</i>	$F_{1,884}=0.64$; $p=0.43$	$F_{1,884}=37.08^{***}$	$F_{97,884}=46.24^{***}$
<i>f0 max</i>	$F_{1,884}=2.38$; $p=0.13$	$F_{1,884}=0.21$; $p=0.65$	$F_{97,884}=105.34^{***}$
<i>f0 end</i>	$F_{1,884}=4.51^*$	$F_{1,884}=6.03^*$	$F_{97,884}=42.02^{***}$
<i>period 1-2</i>	$F_{1,884}=8.09^{**}$	$F_{1,884}=10.36^{**}$	$F_{97,884}=28.81^{***}$
<i>df max 1-2</i>	$F_{1,884}=5.69^*$	$F_{1,884}=24.65^{***}$	$F_{97,884}=19.21^{***}$
<i>q25</i>	$F_{1,884}=0.01$; $p=0.94$	$F_{1,884}=5.40^*$	$F_{97,884}=55.88^{***}$

F–*F*-ratios of GLMM.

Significant effects are given in bold

* $p < 0.05$, ** $p < 0.01$,

*** $p < 0.001$

period 1-2, *df max 1-2*, *f0 max*, and *f0 end* were mainly responsible for sex discrimination.

A DFA classifying alarm calls to age correctly assigned 88.2% (Fig. 2b), exceeding significantly ($p < 0.01$) the random value (53.9%). A separate DFA for males correctly assigned 86.2% to age, and a separate one for females correctly assigned 90.4% to age. In order of decreasing importance, the *f0 st*, *dur st-max*, *dur max-end*, and *period 1-2* were mainly responsible for discrimination.

A DFA classifying alarm calls to individual correctly assigned 90.4% to individual (Fig. 2b), exceeding significantly ($p < 0.01$) the random value (6.0%). A separate DFA for adults correctly assigned 90.3% to individual, a separate DFA for pups correctly assigned 94.7% to individual; a separate DFA for males correctly assigned 94.7% to individual, and a separate DFA for females correctly assigned 93.2% to individual. In order of decreasing importance, the *f0 max*, *dur st-max*, *f0 st*, and *q25* were mainly responsible for discrimination.

Therefore, in *S. fulvus*, assignment to sex was close to the random value; assignment to age was 1.6 times the random value, and assignment to individual as 15 times the random value. Figure 2b summarizes the DFA results for within-species variation of alarm calls in *S. fulvus*. Like *S. suslicus*, individuality in *S. fulvus* calls was more pronounced than age-related cues or sex-related cues. However, in contrast to what we found in *S. suslicus*, we found no single variable important for discrimination of all three the categories: sex, age, and individual identity. Only two variables (*f0 st* and *dur st-max*) were among most important both in DFA for classification to individual and to age, and a single variable (*f0 max*) was among most important both in DFA for classification to individual and to sex. This suggests that, unlike that found in *S. suslicus*, sex- and age-related variation in the alarm call structure were based on acoustic cues unrelated to those responsible for the individual-level variation. Table 5 presents descriptive statistics for *S. fulvus* alarm call variables

included into DFA and body mass for two age classes and two sex/gender classes.

Yellow-bellied marmots (*M. flaviventris*)

Table 6 presents GLMM results for the effects of “sex”, “age”, and “identity” on the alarm call variables in *M. flaviventris*. We found significant effects of identity on all variables and significant effects of sex or age for five of the eight variables. However, in only a few cases, these effects were comparable to the effects of identity (Table 6).

A DFA classifying alarm calls to sex correctly assigned 65.6% to sex (Fig. 2c), exceeding significantly ($p < 0.01$) the random value (57.3%). A separate DFA for adults correctly assigned 69.5% to sex, and one for pups correctly assigned 70.9% to sex. In order of decreasing importance, *duration*, *f peak*, and *f0 end* were mainly responsible for discrimination.

A DFA classifying alarm calls to age correctly assigned 88.9% to age (Fig. 2c), exceeding significantly ($p < 0.01$) the random value (56.5%). A separate DFA for males correctly assigned 92.1% to age, and a separate DFA for females correctly assigned 89.8% to age. In order of decreasing importance, the *duration*, *f0 end*, *f0 max*, and *f0 min* were mainly responsible for discrimination.

A DFA classifying alarm calls to individual correctly assigned 81.6% to individual (Fig. 2c), exceeding significantly ($p < 0.01$) the random value (12.5%). A separate DFA for adults correctly assigned 77.9% to individual; one for pups correctly assigned 88% to individual; one for males correctly assigned 89.9% to individual, and a separate DFA for females correctly assigned 85.1% to individual. In order of decreasing importance, the *duration*, *f0 st*, *d ampl*, *bnd*, and *f0 end* were mainly responsible for discrimination.

Therefore, in *M. flaviventris*, assignment to sex was rather close to the random value; assignment to age was 1.5 times the random value, and assignment to individual was six times the random value. Figure 2c summarizes the DFA results for within-species variation of alarm calls in *M.*

Table 5 Values (means±SD) for the alarm call variables and body weight for age–sex classes of yellow ground squirrels *S. fulvus*

Variable	Males		Females	
	Adults N=25 animals n=247 calls	Juveniles N=25 animals n=247 calls	Adults N=25 animals n=250 calls	Juveniles N=25 animals n=240 calls
<i>dur st-max</i> (ms)	49±9	53±9	47±9	51±7
<i>dur max-end</i> (ms)	20±3	24±6	18±3	24±6
<i>f0 st</i> (kHz)	2.25±0.37	2.64±0.31	2.33±0.34	2.65±0.25
<i>f0 max</i> (kHz)	5.32±0.31	5.19±0.45	5.36±0.46	5.41±0.43
<i>f0 end</i> (kHz)	1.70±0.21	1.59±0.37	1.86±0.24	1.67±0.43
<i>period 1-2</i> (ms)	224±34	204±37	206±25	191±22
<i>df max 1-2</i> (kHz)	0.02±0.18	−0.19±0.27	−0.09±0.18	−0.26±0.28
<i>q25</i> (kHz)	3.81±0.44	3.87±0.37	3.70±0.4	3.97±0.34
<i>Mass</i> (g)	1343±207	309±158	856±138	275±148

flaviventris. Thus, similar to the calls of the two squirrels, in *M. flaviventris*, cues that potentially facilitate individual discrimination were most prevalent, cues that potentially facilitate age discrimination are present, but not as prevalent, and there are few cues that potentially facilitate sex discrimination. Similar to *S. suslicus* but unlike *S. fulvus*, two variables of primary importance were responsible for discrimination in all the three DFA: to sex, to age, and to individual. These results suggest that in *M. flaviventris*, as in *S. suslicus*, the sex- and age-related variation in the alarm call structure was at least partially based on the same acoustic cues as the individual-level variation. Table 7 presents descriptive statistics for the alarm call parameters included into DFA and body mass for two age classes and two sex/gender classes of the *M. flaviventris*.

Comparison of within-species variation among the three sciurids

Figure 3 presents χ^2 -results comparing the DFA values of correct assignment to sex, age, and individual for *S. suslicus*, *S. fulvus*, and *M. flaviventris*. Correct assignment

of calls to sex did not differ between *M. flaviventris* and *S. fulvus* and in both species, were significantly higher of those in *S. suslicus*. Consistently, we found that correct assignment of calls to age did not differ between *M. flaviventris* and *S. fulvus* and in both, were significantly higher than in *S. suslicus*. The value of correct assignment to individual was the highest in *S. fulvus*, the lowest in *S. suslicus*, and intermediate in *M. flaviventris* ($p<0.001$ for all comparisons; Fig. 3).

Discussion

The overall hierarchy of individual-, sex-, and age-related variation in alarm call structure was similar among the three studied species. The alarm calls of these three species permitted reliable discrimination among callers (Blumstein et al. 2004; Sloan and Hare 2006, 2008), but there is relatively less ability to encode age and very little information about sex. In these three species, the features encoding individual identity were more expressed than those encoding group-related features (sex or age). However, as expected, in *S. suslicus*, the individual-, sex-, and

Table 6 GLMM results for effects of factors “sex”, “age”, and “identity” on the alarm call variables in yellow-bellied marmots *M. flaviventris*

Variable	Factor		
	Sex	Age	Identity
<i>Duration</i>	$F_{1,339}=2.75$; $p=0.10$	$F_{1,339}=92.91^{***}$	$F_{82,339}=16.01^{***}$
<i>f0 st</i>	$F_{1,339}=12.61^{***}$	$F_{1,339}=2.79$; $p=0.10$	$F_{82,339}=66.40^{***}$
<i>f0 end</i>	$F_{1,339}=4.28^*$	$F_{1,339}=2.14$; $p=0.15$	$F_{82,339}=28.37^{***}$
<i>f0 max</i>	$F_{1,884}=9.80^{**}$	$F_{1,339}=13.39$; ***	$F_{82,339}=45.07^{***}$
<i>f0 min</i>	$F_{1,884}=5.64^*$	$F_{1,339}=0.07$; $p=0.79$	$F_{82,339}=22.02^{***}$
<i>f peak</i>	$F_{1,884}=8.27^{**}$	$F_{1,339}=12.03^{***}$	$F_{82,339}=30.37^{***}$
<i>d ampl</i>	$F_{1,884}=1.83$; $p=0.18$	$F_{1,339}=1.92$; $p=0.17$	$F_{82,339}=9.01^{***}$
<i>bnd</i>	$F_{1,884}=0.04$; $p=0.84$	$F_{1,339}=15.10^{***}$	$F_{82,339}=10.02^{***}$

F–*F*-ratios of GLMM.

Significant effects are given in bold

* $p<0.05$, ** $p<0.01$, *** $p<0.001$

Table 7 Values (means±SD) for the alarm call variables and body mass for age–sex classes of yellow-bellied marmots *M. flaviventris*

Variable	Males		Females	
	Adults N=12 animals n=60 calls	Juveniles N=26 animals n=129 calls	Adults N=26 animals n=130 calls	Juveniles N=21 animals n=105 calls
<i>Duration</i> (ms)	23±6	38±7	23±5	34±7
<i>f0 st</i> (kHz)	3.63±0.21	3.59±0.38	3.73±0.31	3.97±0.36
<i>f0 end</i> (kHz)	3.35±0.32	3.17±0.46	3.5±0.34	3.40±0.56
<i>f0 max</i> (kHz)	3.75±0.25	3.94±0.43	3.89±0.35	4.30±0.48
<i>f0 min</i> (kHz)	2.49±0.34	2.49±0.44	2.67±0.35	2.71±0.48
<i>f peak</i> (kHz)	3.26±0.19	3.39±0.38	3.43±0.4	3.73±0.38
<i>d ampl</i> (dB)	−16.78±7.5	−17.01±7.52	−20.35±7.27	−19.26±6.25
<i>bnd</i> (kHz)	1.37±0.33	1.36±0.33	1.12±0.23	1.45±0.45
<i>Mass</i> (g)	2976±1130	866±430	2572±713	812±396

age-related characteristics were less prominent than in *S. fulvus* or *M. flaviventris*. In *S. suslicus* and *M. flaviventris*, acoustic features most important for encoding individuality also encode sex and age, suggesting that the individual-level variation is involved in sex- and age-related discrimination. Distinctively, in *S. fulvus*, the sex- and age-related variation was based on unique parameters not used for individual discrimination. Therefore, we can conclude that at least in two ground-dwelling sciurids, the cues encoding the identity of the callers are integral characteristics that are used also for encoding sex and age. At the same time, our data confirmed our hypothesis that, in the two more social species, *M. flaviventris* and *S. fulvus*, alarm calls should provide more cues about caller identity, age, and sex than in the less social species (*S. suslicus*).

In this study, we compared species' DFA results for encoding identity, age, and sex of alarm callers. Because calls are species-specific, we were unable to measure the

same acoustic variables. DFA results are influenced by the similarity of the acoustic variables, the number of the variables included into DFAs, and the number of groups to be discriminated. In the current study, we focused on similar numbers of individuals within each age–sex class and used the same number of acoustic variables per species. These variables were selected by being unrelated and distinctive. Thus, we believe that our DFA results are a valid way to make comparisons among species.

For each individual, we analyzed alarm calls from a single recording session. This experimental design modeled naturally occurring predatory events, where receivers would normally acquire information about attributes of a caller from a single calling bout. Individually discriminable alarm calls could be important to provide information on how many individuals are simultaneously calling (Blumstein et al. 2004; Sloan and Hare 2006, 2008) or may allow tracking of predator movements (Thompson and Hare 2010). However, in *S. suslicus* and *S. fulvus*, the individually distinctive calls could hardly be used to detect false alarm calls and remember the caller. For *S. suslicus* and *S. fulvus*, individuality decreased between calling bouts recorded with time space of 1 year. Reliable identification dropped to as few as 27% to 30% of individuals (Matrosova et al. 2009, 2010a), although this was still greater than expected by chance (Matrosova et al. 2009, 2010a).

The stability of individual acoustic signatures varies between species. Individuality decreases over time in rutting calls of male fallow deer *Dama dama* (Briefer et al. 2010), “boom” calls of male great bitterns *Botaurus stellaris* (Puglisi and Adamo 2004), and chatter calls of bald eagles *Haliaeetus leucocephalus* (Eagle et al. 1989). In some species, individuality is stable but varies with changes in the social environment, as seen in a few captive marmoset species (Jones et al. 1993; Snowden and Elowson 1999; Rukstalis et al. 2003) and in common loons *Gavia immer* (Walcott et al. 2006). Unlikely, individuality is remarkably

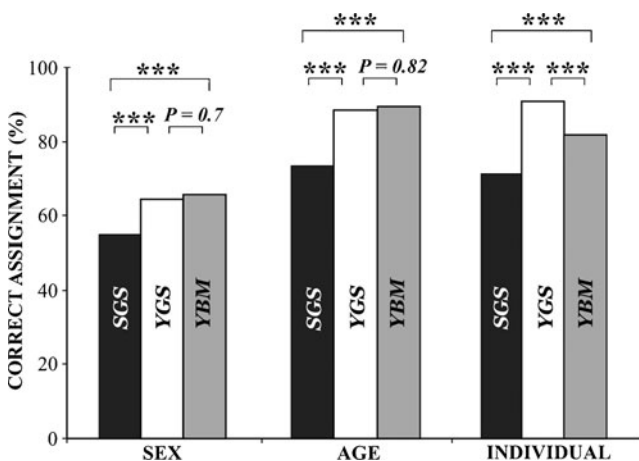


Fig. 3 Comparison between DFA values of correct assignment to sex, age, and individual for speckled ground squirrels *S. suslicus* (SGS), yellow ground squirrels *S. fulvus* (YGS), and yellow-bellied marmots *M. flaviventris* (YBM). ***— $p < 0.001$, χ^2 test

stable across years in calls of eagle owls *Bubo bubo* (Lengagne 2001; Grava et al. 2008) and in the duets of red-crowned cranes *Grus japonensis* (Klenova et al. 2009). Studying the stability of individual acoustic signatures in alarm calls should be extended on a wide range of species of ground-dwelling sciurids, especially in relation to probable use of acoustic fingerprinting as a non-invasive tool for censuses in the field (Terry et al. 2005; Blumstein and Fernández-Juricic 2010; Schneiderová and Policht 2010; Pollard et al. 2010).

Our data suggest that age difference in body mass (Tables 3, 5, and 7), reported previously as one of the main determinants of the fundamental frequency and duration in mammalian calls (Morton 1977; Fitch and Hauser 2002; Matrosova et al. 2007), was relatively less important than variation in the vocal anatomy and/or vocal tuning among individuals. In rapidly maturing ground squirrels, alarm call fundamental frequencies do not differ between juvenile and older animals (Matrosova et al. 2007; Swan and Hare 2008; Volodina et al. 2010). By contrast, in marmots, the fundamental frequency of alarm calls is noticeably higher in juveniles than in adults and thus can indicate the age (Nesterova 1996; Blumstein and Munos 2005; Nikol'skii 2007). Fundamental frequency-based cues to age in marmots might be functionally important in facilitating parental care (Blumstein and Daniel 2004).

In all three species, acoustic cues to sex were least expressed compared with those encoding individual identity and age, probably because knowing a caller's sex is not important in a predatory context. Potentially, the cues to sex should be important in other social contexts, such as post-copulatory mate guarding. Alarm calling during post-copulatory mate guarding has been reported in male Formosan squirrels *Callosciurus erythraeus taiwanensis* and Columbian ground squirrels *Spermophilus columbianus* (Tamura 1995; Manno et al. 2007), but not in any of our species. In other species, emitting alarm calls in mating-related contexts have been reported for male topi antelope *Damaliscus lunatus* which use alarm snorts for retaining estrous females on their territories to secure mating opportunities (Bro-Jorgensen and Pangle 2010) and among birds for ornamented male fowl, *Gallus gallus* (Wilson et al. 2008).

Our results suggest that alarm calls can be reliably discriminated on the basis of individual characteristics in all three species and that the individual-based characteristics appeared to be more prominent than the variation allowing identification of sex and age categories. This potential was related to a species' social structure. However, considering the fact that all species have a rather low level of sociality, it would be interesting to obtain similar data on more social marmot species, such as Alpine marmots (*Marmota marmota*) as well as highly social prairie dogs (*Cynomys* spp.).

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