

Does kinship affect the alarm call structure in the Yellow Ground Squirrel (*Spermophilus fulvus*)?

Ovlivňují příbuzenské vztahy strukturu varovných signálů sysla žlutého (*Spermophilus fulvus*)?

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Abstract. While the closer vocal similarity between mothers and their offspring compared to other conspecifics has been reported in many mammals, e.g. whales, bats and primates, no evidence is available that vocalizations of closely related kin encode relatedness in rodents. In the yellow ground squirrel *Spermophilus fulvus*, females maintain matrilineal kin groups and warn kin of potential predators through alarm calls. In this study, we examine whether the keys to relatedness are presented in the structure of alarm call in this species. Using the Mahalanobis distance, we compared the similarity of structural traits in the alarm calls of 15 related (mother-daughter) and 15 unrelated (adult-juvenile) female dyads in the yellow ground squirrel. No significant differences in the Mahalanobis distance between the two groups were found. In contrast to the keys to relatedness, the keys to individuality have been reported to be strongly expressed in the yellow ground squirrel alarms. With the prevalence of the keys to individuality over the keys to relatedness, kin recognition in the matrilineal groups of this species can be based on the strong keys to individuality. As the prominent individuality of the alarm calls is sufficient to ensure the personalized relations between mothers and daughters, the keys to relatedness may be redundant and not supported by natural selection.

Key words. Rodent, vocal communication, alarm call, kinship, matriline, yellow ground squirrel, *Spermophilus fulvus*.

INTRODUCTION

The closer vocal similarity between mothers and their offspring compared to other conspecifics is usual in mammals experiencing vocal learning (e.g. JANIK & SLATER 1997, 2000). For example, juvenile bottle-nosed dolphins *Tursiops truncatus* share characteristics of their signature whistles with their mothers (TYACK 1997) and juvenile greater horseshoe bats *Rhinolophus ferrumequinum* also share frequency characteristics of their echolocation with their mothers (JONES & RANSOME 1993). Among mammals with genetically predetermined vocal development, evidence of call similarity in closely related kin is available in the group-living primates: e.g. rhesus macaques *Macaca mulatta*, pig-tailed macaques *M. nemestrina* and Campbell's monkeys *Cercopithecus campbelli*, whose calls bear matrilineal characteristics (GOUZOULES et al. 1984, GOUZOULES & GOUZOULES 1990, LEMASSON et al. 2003). In the ground-dwelling sciurids living in matrilineal

kin groups (MICHENER 1983, WATERMAN 2002, POPOV 2007), call similarity between the female kin has not yet been studied.

In species not experiencing vocal learning, the vocal similarity is likely to be linked to the anatomic structure of their vocal apparatus. In mammals, sound is produced at larynx (sound source), then passing through the air cavities of the sound filter (vocal tract, including the throat, oral and nasal cavities). The final call structure depends on the anatomic structure of both components of the vocal apparatus: the sound source and the sound filter (TITZE 1994, FITCH & HAUSER 2002). Probably, in closely related kin, the anatomic structure of their vocal apparatus should be more similar compared to that of other conspecifics, resulting in stronger similarity of calls between relatives. In animals maintaining long-term social relationships, the similarity in calls of relatives may serve as an indicator of relatedness alongside with visual and olfactory features. For example, with screams, the loser rhesus macaques and pig-tailed macaques recruit kin to help them in agonistic conflicts (GOUZOULES et al. 1984, GOUZOULES & GOUZOULES 1990). In rhesus macaques, adult females responded significantly faster and longer to the contact calls of matrilineal relatives (RENDALL et al. 1996).

In our studied species, the yellow ground squirrel (Fig. 1), females maintain matrilineal kin groups (POPOV 2007). This species is a relatively long-living (up to 7 years, A. V. TCHABOVSKY, pers. comm.), diurnal, herbivorous, obligatory hibernating sciurid (ISMAGILOV 1969, EFIMOV 2005). It is the largest of the *Spermophilus* species, with body length without tail of 230–370 mm, body mass at emergence from hibernation of 600–900 g, and body mass before hibernation of 1600–2000 g (ISMAGILOV 1969, EFIMOV 2005, MATROSOVA et al. 2007). Female yearlings are capable of breeding after their first hibernation; while males only after their second hibernation (EFIMOV 2005, POPOV et al. 2006). Mothers maintain prolonged affiliative social contacts with their offspring up to their dispersal or hibernation (STUKOLOVA et al. 2006, STUKOLOVA & TCHABOVSKY 2007). Many of the female yellow ground squirrels hold the same territories for years (SHILOVA



Fig. 1. Adult yellow ground squirrel (*Spermophilus fulvus*) from the Saratov region, Russia; photo by O. BATOVA.

Obr. 1. Dospělý syseľ žlutý (*Spermophilus fulvus*) ze Saratovské oblasti, Rusko. Foto: O. BATOVA.



Fig. 2. Hemipsammophile steppe, the habitat of the yellow ground squirrel situated near Djakovka (Saratov region, Russia), in early June. The lookout is visible in the background; photo by E. VOLODINA.

Obr. 2. Stepní trávníky na pisku, biotop sysla žlutého poblíž obce Djakovka (Saratovská oblast, Rusko) na začátku června. Uprostřed je vidět pozorovatelná. Foto E. VOLODINA.

et al. 2006). Juvenile dispersal is sex-related, with females dispersing at a shorter distance from their natal burrow than males. As a result, spatial clusters of related females – daughters, granddaughters and nieces are created around the adult females (POPOV 2007).

There is no evidence on whether any direct personalized relationships occur in these spatial clusters and whether they are based on vocal communication. Nevertheless, similarly as in other ground-dwelling sciurids, the yellow ground squirrels warn kin of potential predators through alarm calls (SHERMAN 1977, 1981, OWINGS & VIRGINIA 1978, MACEDONIA & EVANS 1993, MATROSOVA et al. 2007). The alarm call is the most usual and the loudest call type in the yellow ground squirrel. The structure of alarm calls is the same in all predatory contexts: towards raptors, terrestrial predators, towards some harmless animals (e.g. hares) and towards humans (NIKOL'SKII 1979, 1984). In the yellow ground squirrel, the alarm call structures are very similar between juveniles and adults that facilitate comparison of call structures between the ages. Unlike in most mammals in which adult calls are lower in frequency, in the yellow ground squirrel the maximum fundamental frequency of the alarm call is lower in juveniles than in adults, in spite of the fact that adults are much larger in size and body mass than juveniles (MATROSOVA et al. 2007).

In our previous study, we found well-expressed individual identity in the alarm calls of the yellow ground squirrel (MATROSOVA et al. in press [b]). However, it is not known whether the keys to relatedness are also encoded in the structure of alarm call in this species. The aim of this study was to compare structural traits of alarm calls between related (mother-daughter) and unrelated (adult-juvenile) female dyads in the yellow ground squirrel.

MATERIALS AND METHODS

Study site and subjects

We recorded the alarm calls during brief capture-recaptures in a natural colony of the yellow ground squirrel in the Saratov region, Russia, near Djakovka (50° 43' 88" N, 46° 46' 04" E) (Fig. 2). Since 2001, this colony has been a subject of a long-term study of behavioral ecology and all animals are regularly captured either with wire-mesh live-traps of original construction, or with kits. All animals are sexed and individually marked with microchips (Bayer AG, Leverkusen, Germany) and dye marked with ursol black D for fur (P-Phenylenediamine) (Rhodia, Paris, France).

Our subjects were 30 free-living female yellow ground squirrels: 15 adults (one-year-old or older) and 15 juveniles; each adult was a mother of one of the juveniles. The mother-daughter relatedness was confirmed on the basis of visual observations on natal emergence, since within the first 2–3 days juveniles stay in a close vicinity to their natal burrow (EFIMOV 2005). Each individual was recorded during a single recording session between the end of May and mid of June in 2005 (10 adults and 10 juveniles) or in 2006 (5 adults and 5 juveniles). The alarm calls of a mother and of her daughter were always recorded in the same year, within two weeks after the natal emergence.

Call recording procedure and equipment

All the recordings were obtained from animals, placed singly in a 30×15×15 cm wire-mesh cage, within one hour after capture. From the cage, animals emitted calls toward a human observer, sitting 2 m from them, either spontaneously or in response to additional stimulation with movements of a hand-held baseball cap. Any stimulation was stopped as soon as the animal started calling. On average, a recording lasted 3–4 min and provided 30–40 alarm call clusters per animal. The distance to the microphone was about 1 m. In cages, the pattern of calling toward humans and the structure of alarm calls were similar to those recorded under natural conditions toward predators (NIKOL'SKII 1979, MATROSOVA et al. 2007), allowing us to reliably distinguish these calls as alarms. Sound recording always preceded other manipulations with the animal (individual mark checking, physical examination and weighing). After the manipulations, the animals were released at the place of capture.

For recordings, we used a Marantz PMD-222 (D&M Professional, Kanagawa, Japan) analog tape recorder with an AKG-C1000S (AKG-Acoustics GmbH, Vienna, Austria) cardioid electret condenser microphone and a Type II chrome audiocassette EMTEC-CS II (EMTEC Consumer Media, Ludwigshafen, Germany). We also used a CF-recorder Marantz PMD-671 with a Sennheiser K6 ME-64 (Sennheiser electronic, Wedemark, Germany) cardioid electret condenser microphone. The systems provided qualitative recording within the range of 40–14,000 Hz and 40–24,000 Hz, respectively.

Call samples

The alarm call consists of tonal notes with the maximum fundamental frequency of 5–6 kHz, depth of frequency modulation of 2.5–3.0 kHz and note duration of about 70 ms, 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 (NIKOL'SKII 1979, ТИТОВ et al. 2005). From most of the 30 recordings (one per animal), we took measurements from 10 randomly selected alarm call clusters of good quality, high amplitude, not broken with wind (5 recordings provided only 5 to 8 clusters). In total, we analyzed 285 alarm call clusters. To avoid pseudoreplication, the individual samples of the alarm call clusters were halved, all even calls making one subset and all odd calls making another subset. Thus each alarm call cluster was used in the analyses only once. The halves (143 and 142 calls respectively) were used to compare the alarm call clusters of related (15 dyads mother-daughter) and unrelated (15 dyads adult-juvenile) females. Each female participated in the unrelated dyad only once with one of unrelated females, selection of females for the unrelated dyads was made randomly.

Table 1. Measured parameters of alarm calls of the yellow ground squirrels
 Tab. 1. Přehled sledovaných parametrů varovných signálů sysla žlutého

parameter	parameter description
<i>f_{st}</i>	the fundamental frequency at the beginning of a 2nd note in a cluster (kHz)
<i>f_{max}</i>	the maximum fundamental frequency of a 2nd note in a cluster (kHz)
<i>f_{end}</i>	the fundamental frequency at the end of a 2nd note in a cluster (kHz)
<i>dur_{st-max}</i>	the time period from the beginning of a 2nd note in a cluster to the point of maximum fundamental frequency of a note (ms)
<i>dur_{max-end}</i>	the time period from the point of maximum fundamental frequency to the end of a 2nd note in a cluster (ms)
<i>quart₁</i>	the value of first energy quartile of a 2nd note in a cluster (kHz)
<i>period₁₋₂</i>	the time period from the beginning of a 1st note to the beginning of a 2nd note in a cluster (ms)
<i>df_{max 1-2}</i>	the difference between the maximum fundamental frequencies of a 1st and 2nd notes in a cluster (kHz)

Call analysis

For the spectrographic analysis, we used Avisoft SASLab Pro software v. 4.3 (Avisoft Bioacoustics, Berlin, Germany). The calls were digitized with 24 kHz sampling frequency and 16-bit precision and high-pass filtrated at 1 kHz to remove background noise. Spectrograms were created using Hamming window, FFT-length 1024 points, frame 50% and overlap 96.87%. These settings provided a bandwidth of 61 Hz, frequency resolution of 23 Hz and time resolution of 1.3 ms.

In the alarm call clusters, we measured 6 note parameters and 2 cluster parameters (Table 1). All measurements were exported automatically to Microsoft Excel (Microsoft, Redmond, WA, USA). Since the first note in a cluster is usually slightly more distinctive by appearance compared to all subsequent notes, which in their order are very similar to each other, we took all the note parameters from a second note in a cluster. Using the screen with the reticule cursor, we measured the following note parameters: 3 fundamental frequency parameters, 2 duration parameters and 1 power spectrum parameter (Table 1, Fig. 3).

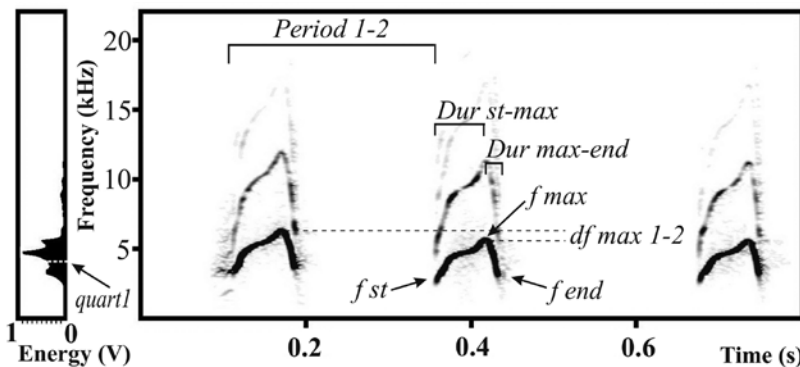


Fig. 3. The alarm call cluster of the yellow ground squirrel and measurements taken in the alarm call notes and clusters (see Table 1 for the description of parameters).

Obr. 3. Varovné signály sysla žlutého s označením měřených parametrů (popis parametrů viz tab. 1).

Also, for each cluster, we measured the time period from the beginning of the first note to the beginning of the second note and calculated the difference between the maximum fundamental frequencies of the first and second notes (Table 1, Fig. 3). We did not measure the interval between alarm call clusters, because this parameter could be influenced by an observer's behavior.

Statistical analyses

With 8 measured call parameters included into the discriminant function analysis (DFA), we calculated the Mahalanobis distances for each of the 30 dyads. The DFA analysis was made separately for the related and unrelated dyads, with 30 animals included into each analysis. The Mahalanobis distances were used as a measure of similarity in the structure of alarm calls between adults and juveniles. The lower was the value of Mahalanobis distance between the alarm call subsets of two individuals, the greater was the similarity in the structure of their alarm calls. We used the Mann-Whitney U-test to compare two samples of the Mahalanobis distances, of the related and of the unrelated dyads. All statistical analyses were made with STATISTICA, v. 6.0 (StatSoft, Tulsa, OK, USA), and differences were considered significant where $p < 0.05$.

RESULTS AND DISCUSSION

No significant differences in the Mahalanobis distance between the related and unrelated female dyads were found (Mann-Whitney test, $U=96$, $p=0.49$). Nevertheless, a slight trend toward the higher similarity in the structure of alarm calls of the related females compared to unrelated was found (Fig. 4).

These data suggesting the absence of the within-family similarity in the structure of alarm calls indicate the irrelevance of vocal keys for kinship recognition in the yellow ground squirrel.

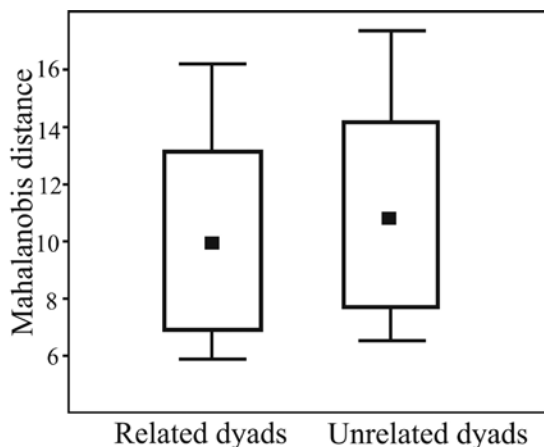


Fig. 4. The average Mahalanobis distances for the alarm calls, recorded in the related (mother-daughter, $n=15$) and unrelated (adult-juvenile, $n=15$) female dyads of the yellow ground squirrel. Central points show means, boxes \pm SD, whiskers minimum and maximum values.

Obr. 4. Hodnoty Mahalanobisovy vzdálenosti varovných signálů zjištěné mezi příbuznými (matka – dcera, $n=15$) a nepříbuznými samicemi (dospělá samice – mládě, $n=15$) sysla žlutého.

To date, the kin-specific alarms have not been reported for any ground-dwelling sciurids. At the same time, there is evidence in many ground-dwelling sciurids that the alarm calls encode individuality and age. Strong individuality encoded in the alarm calls has been reported for steppe marmots *Marmota bobak* (NIKOL'SKII & SUCHANOVA 1994), yellow-bellied marmots *M. flaviventris* (BLUMSTEIN & MUNOS 2005), Belding's ground squirrels *Spermophilus beldingi* (LEGER et al. 1984, McCOWAN & HOOPER 2002) and speckled ground squirrels *S. suslicus* (VOLODIN 2005, MATROSOVA et al. in press [a]). Consistently, discrimination between familiar and unfamiliar vocalizations in playback experiments has been found in the Richardson's ground squirrel *S. richardsonii* (HARE 1998) and the yellow-bellied marmot (BLUMSTEIN & DANIEL 2004). Discrimination between juvenile and adult calls has been observed in California ground squirrels *S. beecheyi* (HANSON & COSS 2001), steppe marmots (NESTEROVA 1996) and yellow-bellied marmots (BLUMSTEIN & DANIEL 2004).

Among ground-dwelling sciurids, the prevalence of the keys to individuality over the keys to age in the alarm calls has been reported for yellow ground squirrels (MATROSOVA et al. in press [b]) and for yellow-bellied marmots (BLUMSTEIN & MUNOS 2005). At the same time, the keys to age are only poorly expressed in the alarm calls of yellow ground squirrels (MATROSOVA et al. 2007). According to the current data, in the yellow ground squirrel the keys to individuality prevail also over the keys to relatedness. Thus, kin recognition in the matrilineal groups of this species may be based on the strong keys to individuality *per se*. While the prominent individuality of the alarm calls is sufficient to ensure the personalized relations between mothers and daughters, the keys to relatedness may be redundant and hence not supported with natural selection.

SOUHRN

Zatímco u vokálních projevů mnoha druhů savců, např. kytovců, netopýrů a primátů, již byla zaznamenána větší podobnost mezi matkami a jejich potomky než mezi nepřibuznými jedinci, nebylo dosud prokázáno, že by vokalizace odrážela příbuznost jedinců u nějakého druhu hlodavců. Samice sysla žlutého (*Spermophilus fulvus*) se zdržují v matrilinéárních příbuzenských skupinách a vydávají akustické varovné signály, aby varovaly své příbuzné před potenciálními predátory. Cílem této práce proto bylo zjistit, zda struktura varovných signálů tohoto druhu obsahuje informaci o příbuznosti jedinců. S použitím Mahalanobisovi vzdálenosti jsme porovnali podobnost několika strukturálních znaků varovných signálů 15 příbuzných (matka-dcera) a 15 nepřibuzných (dospělec-juvenil) samičích dvojic. Neodhalili jsme žádné významné rozdíly v Mahalanobisově vzdálenosti mezi těmito dvěma skupinami. Akustická struktura varovných signálů silně odráží individuální rozdíly mezi jedinci, nikoliv však jejich vzájemnou příbuznost. Rozpoznávání příbuzných jedinců v matrilinéárních skupinách u tohoto druhu by proto mohlo být založeno na těchto velkých individuálních rozdílech. Markantní individuální rozdíly ve varovných signálech jsou tedy možná dostačující ke spolehlivému rozpoznání vzájemných vztahů mezi matkami a dcerami, a proto jsou další informace o jejich příbuznosti obsažené ve varovných signálech možná nadbytečné a jejich vznik nebyl podporován přírodní selekcí.

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