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Population density does not affect the alarm call characteristics in the Speckled Ground Squirrel (*Spermophilus suslicus*)

Populační hustota neovlivňuje vlastnosti varovných signálů sysla perličkového (*Spermophilus suslicus*)

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Abstract. While the environmental effects on animal vocalizations have been studied in many birds, mammals and in particular in the ground-dwelling sciurids, the influence of social surrounding on the call structure is poorly understood. The main idea we test here is that in the animals using alarm calls to warn kin of potential predators, vocal characteristics could be adjusted according to the changes in interindividual distances between conspecifics. At higher population density, the distance between individuals becomes shorter. The increasing frequency of the alarm calls will make them less perceptible to predators, as they will propagate at shorter range compared to the lower-frequency ones. In this study, we compare alarm call characteristics of 28 speckled ground squirrels repeatedly tested in years with low and high population density. Whereas population density decreased three times in the three subsequent study years, fundamental frequency of the alarm calls did not decrease in response to the increase of the interindividual distance. Our findings suggest that speckled ground squirrels do not adjust characteristics of their alarm calls to the shortening distance between conspecifics.

Key words. Rodent, vocal communication, alarm call, population density, speckled ground squirrel, *Spermophilus suslicus*.

INTRODUCTION

Many species of mammals use alarm calls to warn kin of potential predators. The alarm calls have been reported for ungulates (Reby et al. 1999), carnivores (Manser 2001), primates (Seyfarth et al. 1980, Fichtel & Kappeler 2002) and are very prominent in the ground-dwelling sciurids (Sherman 1977, 1981, Owings & Virginia 1978, Macedonia & Evans 1993, Blumstein 2007, Matrosova et al. 2007). Thorough investigation of alarm vocal behaviour in the ground-dwelling sciurids resulted in the appearance of a few hypotheses, connecting acoustic characteristics of the calls to their probable function. For example, according to the hypothesis about the effects of habitat complexity (height of vegetation, diverse topography etc.) on call structure, the time-frequency characteristics of alarm calls are adapted to their optimal propagation through the environment (Slobodchikoff & Coast 1980, Nikol'skii 1984, Perla & Slobodchikoff 2002, Blumstein 2007). Within habitats, social factors such as population density can also affect the acoustic characteristics of the alarm calls. We can suppose that at high population density, animals should increase frequency of their alarm calls to make them less perceptible to predators. This reasoning follows the fact that higher-frequency calls show quicker attenuation and propagation at shorter distances compared to the lower-frequency ones (Wiley & Richards 1978). Thus, the higher frequency of alarm calls emitted at shorter distances towards conspecifics, that usually are closely related kin (e.g. Sherman 1981, Waterman 2002, Popov 2007), should reduce the range of sound propagation and decrease the risk of predation (e.g. Wilson & Hare 2006).

Nevertheless, direct evidence on the influence of social density on alarm calling is scarce. The available quantitative data are related mostly to the relative vocal activity toward humans or toward natural predators, but not to the acoustic structure of the alarms. They are mostly restricted to the notices that, in some rodents and lagomorphs, alarm vocalization decreases significantly as a result of an abrupt fall in the population density after deratization (see review in Schilova

Fig. 1. Adult speckled ground squirrel (*Spermophilus suslicus*) from the south of the Moscow region, Russia (photo by V. Matrosova).
Obr. 1. Dospělý sysel perličkový (*Spermophilus suslicus*) z jihu Moskevské oblasti, Rusko (foto: V. Matrosova).

1993). For example, it is reported for a natural population of the Pallas' pika *Ochotona pallasi* that the decline of population density from 7.2 to 0.3 individuals/ha resulted in decreasing percentage of alarm callers among the observed animals from 60.7% to 5.3%. In the same species, after the removal of 70% of 90 individuals from the experimental study grid, the number of calls produced toward predators per hour decreased from 4.06 to 2.26 (Schilova 1993).

The object species of this study, the speckled ground squirrel (Fig. 1), is a relatively long living (up to 6 years, Babitsky et al. 2006), small-sized (body mass 180–220 g, body length without tail 190–220 mm), diurnal, herbivorous, obligate hibernating sciurid (Lobkov 1999). Yearlings are capable of breeding after their first wintering (Babitsky et al. 2006). The alarm call of the speckled ground squirrel consists of weakly modulated tonal notes of about 200 ms in duration, with the fundamental frequency ranging from 8500–11500 Hz, which are typically produced in series with intervals substantially longer than the duration of the notes themselves (Nikol'skii 1979, Volodin 2005, Matrosova et al. 2007).

In natural colonies of this species, population density can vary largely between years, ranging from a few to as much as 300 individuals per hectare (Lobkov 1999, Babitsky et al. 2006). At low population density, speckled ground squirrels can live in close vicinity to each other, forming spatial aggregations, separated with plots of rarefied population density (Shekarova et al. 2003). Therefore, this species provides a convenient model to test the effects of population density on the alarm call structure.

Speckled ground squirrels inhabit open grassland habitats, and a month after emergence from hibernation the grass is already so tall and dense that a squirrel standing upright is perfectly hidden. The adaptation supposed in this study (a shift of the fundamental frequency toward higher values at higher population density) should be irrelevant against aerial predators, but it may be relevant against terrestrial predators, in particular weasels *Mustela nivalis* (Lobkov 1999), which cannot see the squirrels in the dense grass or locate them by smell from a distance. Thus, they may rely on hearing the speckled squirrels' alarm calls. In this case, the dependence of the alarm call fundamental frequency on population density may be adaptive. The aim of this study was to estimate the supposed shifts in acoustic traits of alarm calls in response to variation of population density, occurring throughout three study years in a natural colony of the speckled ground squirrel.

MATERIAL AND METHODS

Study site, dates and subjects

The study was conducted during periods of the aboveground activity of the speckled ground squirrels, in a 1-hectare study grid of a free-living colony. The site is situated in the Moscow region, Russia (54° 47' 68" N, 38° 42' 23" E) and is one of the northernmost colonies of the species (Shekarova et al. 2003). The aboveground activity of the colony lasts 3.5–4 months each year, from early or mid April to early or mid August (Tchabovsky et al. 2005). The study grid is situated on a low riverbank, 50 m apart from the shoreline (Fig. 2).

The data on population density were collected from mid April to early August 2003–2005, and the acoustic data from mid April to mid May 2003–2005. The study years were a period of strong population decline in the colony, so the population densities differed strongly between each two sequential study years.

Our subjects were 134 speckled ground squirrels, living in the study grid in 2003–2005. Of them, 106 individuals were included only in the analysis of population density in the study grid, 15 individuals only in the analysis of alarm calls and 13 (9 males, 4 females) were included in both analyses.

Population density analysis

The study colony is subject to a long-term study of behavioral ecology since 2001 (Tchabovsky et al. 2005, Babitsky et al. 2006). All animals in this colony are individually marked with microchips (Bayer AG, Leverhusen, Germany) and repeatedly (once every two weeks or more often) captured-recaptured in wire-mesh live traps 30x10x10 cm with sunflower seed bait, followed by acoustic recording (Matrosova et al. in press).

We used 20–25 live traps exposed simultaneously and checked them every 1–1.5 hour. The live traps were distributed evenly over the study grid, each of them being installed at the entrance to an inhabited burrow, indicated by the presence of cut grass and fresh feces near the entrance. After capture, the live trap was moved to another burrow. If no animal was captured within a few hours, the trap was also moved to another burrow. Within 2–3 days of a capturing session, each burrow in the study grid was live-trapped 2–3 times. The number of individuals captured once during a session was always higher than the number of individuals captured two or three times.

The geographical coordinates of capture points were taken using the GPS navigator Garmin 12 (Garmin Ltd., Olate, Kansas, USA). In the individuals for which the coordinates were available for three or more captures within a year, we calculated the sizes of their individual territories and determined coordinates of their centers with ArcView 3.3 software (ESRI Inc., Redlands, California, USA), applying the minimum convex polygon – MCP procedure (Shoener 1981).

As a measure of population density we used a total number of adult (overwintered) individuals, captured within a study year in the experimental study grid, and the distance to the nearest neighbor (i.e. the minimum distance between the centers of the individual territories). In total, the distances to the nearest neighbor were calculated for 119 individuals: for 31 males and 21 females in 2003, for 26 males and 18 females in 2004 and for 14 males and 9 females in 2005.

Fig. 2. Habitat of the speckled ground squirrel on the lower bank of the Osetr river (Moscow region, Russia) in early May (photo by I. Volodin).
Obr. 2. Biotop sysla perličkového na břehu řeky Osetr (Moskevská oblast, Rusko) na začátku května (foto: I. Volodin).

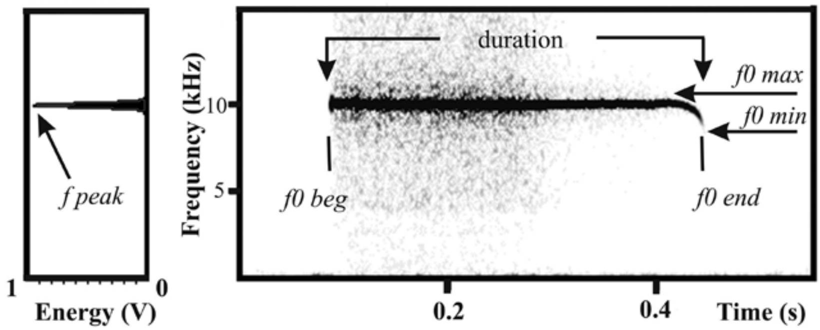

Fig. 3. Measured alarm call parameters in the speckled ground squirrel. Left – power spectrum, right – spectrogram. *Duration* – call duration, *f peak* – frequency of maximum amplitude, *f max* – maximum, *f min* – minimum, *f st* – start, and *f end* – end fundamental frequency.
Obr. 3. Měřené parametry varovných signálů sysla perličkového. Vlevo – power spektrum, vpravo – spektrogram, *duration* – celková délka signálu, *f peak* – frekvence maximální amplitudy, *f max* – maximální, *f min* – minimální, *f st* – počáteční a *f end* – konečná základní (fundamentální) frekvence.

Call recording procedure and equipment

The alarm calls were recorded from animals present in wire-mesh traps within 1 hour of capture. The animals emitted alarm calls toward a human observer, sitting 1 m from them, either spontaneously or in response to additional stimulation (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 calls per animal. The distance to the microphone was about 30 cm. In live traps, 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, Volodin 2005, 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). The system provided qualitative recording within the range of 40–14,000 Hz.

Call analysis

The alarm calls recorded from individuals for which the alarm call samples were available for two sequential study years (one recording session per animal per year) were included in the analysis. In total, we analyzed alarm calls of 28 individuals: 10 males and 1 female in 2003 and 2004, and 6 males and 11 females in 2004 and 2005. From each recording session we selected 10 calls of good quality (in 6 recording sessions only 4 to 7 alarm calls). In total, we analyzed 534 alarm calls in 56 recording sessions from 28 individuals.

For the spectrographic analysis, we used the 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.

For each alarm call, we measured the maximum, minimum, start and end values of the fundamental frequency, maximum amplitude frequency and duration (Fig. 3). All measurements were exported automatically to Microsoft Excel (Microsoft, Redmond, WA, USA).

Statistical analyses

We used the Wilcoxon matched pairs test to compare the mean parameter values for calls recorded in the two subsequent years. We used the Mann-Whitney U-test to compare the distances to the nearest neighbor between the two subsequent years. Also, for the 13 individuals, which provided both call recordings and the distances to the nearest neighbor, we compared the spatial and acoustic data using the Sign test. 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

In the study grid, population density of speckled ground squirrels decreased progressively from year to year, from 300 individuals per hectare in 2003 to 216 in 2004 and 100 in 2005 (Fig. 4). The distance to the nearest neighbor increased accordingly (differences between 2004 and 2005 were significant, Mann-Whitney U-test, $U=259$, $p<0.01$, $n_1=44$, $n_2=23$) (Fig. 4). However, frequency parameters of the alarm calls did not show the expected decrease with the increase of the interindividual distance (Table 1). Neither the duration of alarm calls showed any trends

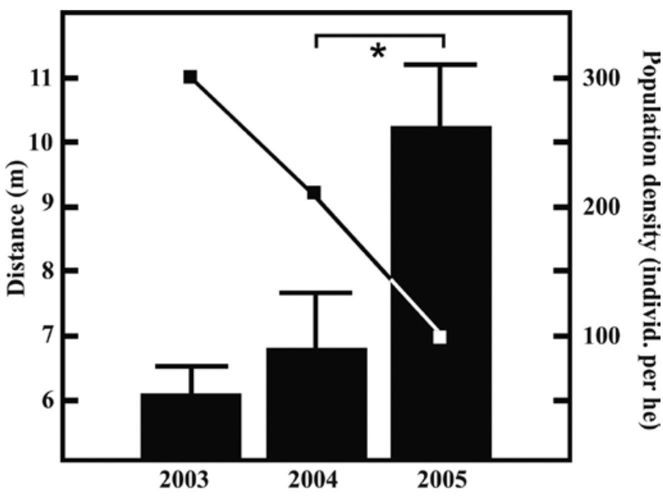

Fig. 4. Distance to the nearest neighbor (bars show averages, boxes ± SE) and population density (line) of the speckled ground squirrels in the one hectare study grid during the three study years; * – differences are significant, Mann-Whitney U-test, $p<0.01$.
Obr. 4. Vzdálenost k nejbližšímu sousedovi (příčky ukazují průměry, boxy ± SE) a hustota populace (přímka) sysla žlutého na jednohektarové studijní ploše v průběhu tří let; * – rozdíly jsou signifikantní, Mann-Whitney U-test, $p<0.01$.

Table 1. Values (mean±SD) of the alarm call parameters in the 28 studied speckled ground squirrels and results of their comparison with the Wilcoxon matched pairs test; *f peak* – frequency of maximum amplitude, *f max* – maximum fundamental frequency, *f min* – minimum fundamental frequency, *f st* – start fundamental frequency, *f end* – end fundamental frequency

Tab. 1. Hodnoty (průměr ± SD) parametrů varovných signálů 28 studovaných jedinců sysla perličkového a výsledky jejich srovnání pomocí Wilcoxonova párového testu: *f peak* – frekvence s maximální amplitudou, *f max* – maximální základní (fundamentální) frekvence, *f min* – minimální základní (fundamentální) frekvence, *f st* – počáteční základní (fundamentální) frekvence, *f end* – konečná základní (fundamentální) frekvence

call parameter	comparison between 2003–2004 (n=11)			comparison between 2004–2005 (n=17)		
	2003	2004	*p*	2004	2005	*p*
duration (ms)	226±58	224±57	0.42	261±63	247±65	0.16
f peak (kHz)	9.61±0.70	9.76±0.51	0.53	9.50±0.71	9.29±0.62	0.16
f max (kHz)	9.78±0.70	9.93±0.56	0.53	9.66±0.74	9.44±0.67	0.24
f min (kHz)	9.42±0.67	9.53±0.53	0.66	9.18±0.71	9.02±0.69	0.69
f st (kHz)	9.68±0.72	9.83±0.56	0.59	9.51±0.80	9.30±0.69	0.27
f end (kHz)	9.51±0.71	9.62±0.64	0.59	9.28±0.76	9.11±0.76	0.69

according to the changes in population density. Only in 9 of 13 individuals the changes of the distance to the nearest neighbor and the maximum fundamental frequency of alarm calls were inversely related (the hypothesis is not supported, Sign test, Z=1.11, p=0.27). Therefore, speckled ground squirrels do not shift the time and frequency characteristics of their alarm calls with changes in the proximity to their conspecific neighbors.

There is a lot of evidence that adult animals can change their call structure under variable environment conditions. Song birds produce more intensive and prolonged songs and calls under enhanced background noise (Brumm & Todt 2002). The same effect has been reported for common marmosets *Callitrix jaccus* (Brumm et al. 2004). The California ground squirrels *Spermophilus beecheyi* living along noisy highways increase the maximum amplitude frequency of their calls compared to their conspecifics living under low-noise conditions (Rabin et al. 2003). The Carolina wrens *Thryothorus ludovicianus* change characteristics of their songs after the appearance of leaves on trees, which affect the acoustic characteristics of their environment (Naguib 1996). Male common loons *Gavia immer* that switched their last-year territories also change their individually distinctive "yodel" calls, while the birds staying in their home territories retain their calls unchanged (Walcott et al. 2006). Changes in calls following the changes in social surrounding have been reported for pygmy marmosets, *Cebuella pygmaea* (Snowdon & Elowson 1999, Snowdon 2001) and for Wied's marmosets *Callithrix kuhlii* (Rukstalis et al. 2003).

Lack of adjustment in the call frequency is not a result of inability of speckled ground squirrels to tune the fundamental frequency of their alarm calls. In a previous study we found that fundamental frequencies of alarm calls are undistinguishable between adult and juvenile speckled ground squirrels, in spite of the fact that the adults are much larger in size (Matrosova et al. 2007). We hypothesized that juveniles mimic the alarm call frequency of adults to avoid infanticide and predation from the age-specific predators that are dangerous only for the juveniles but not for adults (Matrosova et al. 2007). Consistently, we found that the adult speckled ground squirrels can widely change the values of the time and frequency variables of their alarm calls, both within a breeding season and from year to year (Matrosova et al. 2009). The results of the present study suggest that population density should probably be excluded from the set of factors that are responsible for the high long-term variability of the alarm calls in the speckled ground squirrel.

However, further research is needed to extend the results on free-living animals. Alarm calls in our study were recorded from animals caught in traps, which might impose an effect on our results. However, our unpublished data on free-living yellow ground squirrels *Spermophilus fulvus* validate the applied method (i.e. gathering alarm calls from ground squirrels captured in live traps calling toward a human observer). These results show no differences in variation of alarm call structures, whether they are recorded twice from dye-marked individuals calling toward humans from a live trap or twice from individuals calling from the field. That is, the factor of recording (live trap or field) does not affect significantly the structure of vocal parameters being analyzed. However, this sort of validation is available only for the related yellow ground squirrel, as it is larger and lives in less dense grass than the speckled ground squirrel, so the animals can be dye-marked and observed visually.

SOUHRN

Účinky prostředí na vokalizaci zvířat byly studovány u mnoha druhů ptáků a savců, včetně pozemních veverkovitých hlodavců, o vlivu sociálních faktorů na strukturu varovných signálů však zatím víme velmi málo. V této studii je testována hypotéza, že akustická struktura varovných signálů, sloužících k upozornění příbuzných jedinců na přítomnost predátora, může být přizpůsobována změnám ve vzdálenostech mezi jednotlivými jedinci v kolonii. Při vyšší populační hustotě se zkracuje vzdálenost mezi jednotlivými zvířaty. V této situaci mohou varovné signály s vyšší frekvencí snižovat jejich nápadnost pro predátory, protože se ve srovnání s nízkofrekvenčními signály šíří na kratší vzdálenost. V práci jsou srovnávány varovné signály 28 jedinců sysla perličkového, opakovaně testovaných v letech s nízkou a vysokou populační hustotou. Zatímco populační hustota se v průběhu tří po sobě jdoucích let třikrát snížila, nedošlo ke snížení základní (fundamentální) frekvence varovných signálů, které by odpovídalo zvýšení vzdáleností mezi jednotlivými jedinci v kolonii. Výsledky studie nasvědčují tomu, že u sysla perličkového nedochází se změnou populační hustoty a měnícími se vzdálenostmi mezi sousedními jedinci v kolonii ke změnám jejich varovných signálů.

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