

One plus one: Binary alarm calls retain individual signature for longer periods than single-note alarms in the European ground squirrel (*Spermophilus citellus*)



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ABSTRACT

Ground squirrels emit species-specific alarm calls that, among other characteristics, differ by the number of elements. Unlike some species that produce single-element calls, e.g., the Speckled ground squirrel (*Spermophilus suslicus*), individual European ground squirrels (*S. citellus*) frequently emit binary-element calls in addition to single-element calls. We tested the hypothesis that the time stability of individuality encoded in alarm calls might be better retained by complicating their acoustic structure by adding extra elements. In a semi-captive colony of individually marked European ground squirrels, we repeatedly recorded alarm calls that were produced towards a human by 12 adult (2 males and 10 females) live-trapped animals. Repeated recordings occurred within time spans of a few hours, 2 days and 1 year from the first recording. Our results showed that individual calls were highly similar within recordings, but less similar between recordings separated by time spans. Individual differences were best retained when we used nine acoustic variables from both elements. The differences were worse when we used nine variables from only the first element and worst when we used nine variables from only the second element. These results supported the caller reliability hypothesis for species that produce multiple-note alarms, e.g., the Richardson's ground squirrel (*S. richardsonii*).

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1. Introduction

Extensive research exploring individuality encoded in vocalizations of mammals has contributed to our understanding of their social, reproductive and anti-predator behaviours. Calls that are highly stereotyped within individuals, but highly variable among individuals at the same time, have been reported for many mammalian taxa, including insectivores (Schneiderová and Zouhar, 2014), bats (Gillam and Chaverri, 2012), rodents (Matrosova et al., 2011), lagomorphs (Conner, 1985), carnivores (Frommolt et al., 2003; Volodina et al., 2006; Palacios et al., 2007; Smirnova et al., 2016), pinnipeds (Phillips and Stirling, 2000; Charrier et al., 2002, 2010), ungulates (Vannoni and McElligott, 2007; Volodin et al.,

2011; Sibiryakova et al., 2015), cetaceans (Janik et al., 2006), primates (Zimmermann and Lerch, 1993; Mitani et al., 1996; Ceugniet and Izumi, 2004), hyraxes (Koren and Geffen, 2011) and manatees (Sousa-Lima et al., 2002). Individual signatures may promote reliable vocal recognition between mother and offspring (Terrazas et al., 2003; Torriani et al., 2006; Charrier et al., 2010; Briefer and McElligott, 2011; Knörnschild et al., 2013; Sibiryakova et al., 2015), breeding mates (Zimmermann and Lerch, 1993; Reby et al., 2006; Russ and Racey, 2007), members of social groups (Mitani et al., 1996; Blumstein and Daniel, 2004; Hartwig, 2005; Janik et al., 2006; Volodina et al., 2006; Gillam and Chaverri, 2012) and neighbours (Conner, 1985; Frommolt et al., 2003). In colonially living ground-dwelling sciurids, individually distinctive alarm calls allow colony members to estimate the degree of danger by associating individual identity with the caller's past reliability as an alarm signaler (Hare and Atkins, 2001; Blumstein et al., 2004; Sloan and Hare, 2008; Matrosova et al., 2009; Thompson and Hare, 2010). Individual signatures may also have important applications in management and conservation since they allow the non-invasive discrimination and

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To date, the time stability of acoustic individual features has only been studied in the speckled and yellow ground squirrels (Matrosova et al., 2009, 2010a, 2010b). The present study is the first study examining the time stability in a ground squirrel species with alarm calls comprising two structurally different elements, the European ground squirrel. The aim of the study was to estimate the stability of individual features encoded in the structure of alarm calls of this ground squirrel species after three different time spans: several hours, two days, and one year. We aimed to estimate not only the effect of the time span between the repeated recordings but also the impact of the two elements in the stability of the callers' vocal identity.

2. Materials and methods

2.1. Study site and colony

We conducted the research in a semi-natural outdoor enclosure located at the Prague Zoo (50°7'16.8"N, 14°24'11.0"E), under the Action Plan for the European Ground Squirrel in the Czech Republic and under the permission of the Český kras protected landscape area, no. 00225/CK/E/06. The enclosure is located within an area naturally inhabited by the European ground squirrels until the 1960s (Vohralík and Řeháková, 1985). The 140 m² (14.5 m × 9.5 m × 2 m) enclosure was built in 2006 in frames of the Action Plan for the Conservation of the European Ground Squirrel in the Czech Republic. The European ground squirrel is currently listed by the International Union for Conservation of Nature (IUCN) as a vulnerable species in Europe (Coroiu et al., 2008) and as critically endangered in the Czech Republic (Anděra and Červený, 2003). Recent conservation efforts for preventing the extinction of this species in the Czech Republic include establishing semi-captive colonies as potential reservoirs of animals for subsequent reintroductions (Matějů et al., 2010; Schneiderová et al., 2015).

Seventy-three European ground squirrels, including 33 males and 40 females, originating from four natural populations (Prague Letňany, airfield, 50°7'52.6"N, 14°31'31.5"E; Raná, National Nature Reserve, 50°24'25.3"N 13°46'16.5"E; Raná Hrádek, airfield, 50°24'13.9"N 13°45'07.0"E; and Bezděčín, airfield, 50°23'53.9"N 14°53'54.5"E) located in the Czech Republic were individually marked with microchips (Planet ID, Essen, Germany) and gradually introduced into the enclosure from 2006 to 2011. We documented the successful breeding of the introduced population in 2008–2010, 2012, and 2014. At the end of the ground squirrel aboveground season, lasting from March to September, the enclosure was inhabited by approximately 50 individuals in 2012, approximately 60 individuals in 2013, and approximately 50 individuals in 2014. During their aboveground season, the ground squirrels were provided with carrots, beets, cereals, apples and seeds *ad libitum*.

2.2. Call collection

The alarm calls of ground squirrels were recorded from 9 am to 6 pm during June and July in 2012–2014. Ground squirrels were recorded and then re-recorded when they were trapped in custom-made wire-mesh live traps (15 cm × 15 cm × 48 cm and 14 cm × 12 cm × 44 cm) that were baited with apples and carrots. In these traps, the ground squirrels emitted alarm calls spontaneously towards a researcher (IS) standing or walking near the trap. This recording procedure is generally accepted for ground-dwelling sciurids (Hanson and Coss, 2001; Blumstein and Daniel, 2004; Blumstein and Munos, 2005; Matrosova et al., 2009, 2010b) because the alarm calls collected from live-trapped individuals are indistinguishable acoustically from those produced by free-ranging individuals (Matrosova et al., 2010a).

The alarm calls were recorded with the solid state recorder Marantz PMD-661 (D&M Professional, Kanagawa, Japan) with built-in microphones (recording format: 16-bit, 44.1 kHz; frequency response: 20–20,000 Hz). After the recording procedure, which lasted from five to ten minutes, each animal was removed from the trap, sexed and its microchip number was scored. Then, the animal was released into the burrow in the immediate vicinity of the place where it was live-trapped and recorded.

2.3. Animal and call samples

In total, 12 individuals (2 males and 10 females) provided calls for this study (Table 1). Previous studies demonstrated that male and female alarm calls of some ground-dwelling sciurids did not differ significantly (Volodin, 2005; Matrosova et al., 2011, 2012); therefore, we pooled males and females in our data sets. We created three data sets of calls: 1) an "over-hours" data set including 7 individuals, which were re-captured and re-recorded within a time span of several hours; 2) an "over-days" data set including 7 individuals, which were re-captured and re-recorded within a time span of two days; and 3) an "over-year" data set including 7 individuals, which were re-captured and re-recorded within a time span of one year, after hibernation. Eight ground squirrels from the total of 12 individuals provided calls for more than one data set (Table 1). We took different alarm calls for each data set in cases when the calls of a particular individual were included in more than one data set to decrease the potential pseudoreplication.

For each individual, we randomly selected from 10 to 15 alarm calls of high quality (with high signal-to-noise ratio and uninterrupted by wind) from the preceding recordings and took similar or equal lengths of alarm calls from the subsequent recordings (over-hours, over-days, and over-year). The over-hours data set included 186 calls from individuals that were recorded twice within a time span of a few hours. The over-days data set included 185 calls from individuals that were recorded twice within a time span of two days. The over-year data set included 192 calls from individuals recorded twice within a time span of one year (Table 1). A total of 563 selected alarm calls were visualized and labelled using a waveform and spectrogram in Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany) with the following settings: Hamming window, FFT length 512, frame size 50% and overlap 93.75%.

2.4. Call analysis

All of the alarm calls recorded from the subject animals contained two elements (Schneiderová and Policht, 2012). We used the "automatic parameter measurements" tool in Avisoft SASLab Pro to measure 10 (two temporal, eight frequency) acoustic variables per each of the two elements of each alarm call (Fig. 1). The two temporal variables were the element duration (*dur*) and the distance from the start to the maximum amplitude point of the element (*disttmax*). Eight frequency variables, measured from the lowest (fundamental) harmonic band (*f0*), were the start frequency (*f0 start*), the end frequency (*f0 end*), the midpoint frequency (*f0 center*), the frequency at the point of the maximum amplitude (*f0 maxamp*), the mean frequency of the entire element (*f0 mean*), the minimum bandwidth frequency (*fbnd min*), the maximum bandwidth frequency (*fbnd max*), and the relative standard deviation of the entire element (*f0 std*). This variable was extracted by the software as the standard deviation/mean value of frequencies computed for all spectra between the start and the end of the element, and this was used in the present study to quantify frequency modulation.

We calculated the location of the maximum amplitude point along the element duration (*peak loc*) as *disttmax/dur* and the bandwidth of the fundamental harmonic band (*fbnd*) as *fbnd max*

Table 1
The number of alarm calls recorded from individual European ground squirrels during captures and re-captures made with time spans of several hours (“over-hours”), of two days (“over-days”) and of one year (“over-year”). Preceding = calls recorded during the preceding (first in order) capture. Subsequent = calls recorded during the subsequent (second in order) capture. Abbreviations: M = male; F = female.

Individual	Over-hours		Over-days		Over-year		Total calls
	Preceding	Subsequent	Preceding	Subsequent	Preceding	Subsequent	
F418044	15	15	10	15	15	11	81
F34888	13	15	–	–	15	15	58
F854982	13	10	10	15	–	–	48
F34237	15	15	–	–	–	–	30
F46191	11	10	–	–	15	14	50
F420663	–	–	12	15	15	15	57
F848552	–	–	15	15	15	15	60
F34567	–	–	11	10	15	10	46
F31605	–	–	15	15	–	–	30
F95186	–	–	–	–	10	12	22
M845415	15	11	12	15	–	–	53
M418114	13	15	–	–	–	–	28
Total calls	95	91	85	100	100	92	563

– *fbnd min*. All of the measurements were exported automatically to Microsoft Excel (Microsoft Corp., Redmond, Washington). Only 9 acoustic variables (*dur*, *peak loc*, *f0 start*, *f0 end*, *f0 center*, *f0 max-amp*, *f0 mean*, *f0 std*, and *fbnd*) per each element were included in subsequent statistical analyses.

2.5. Statistics

Statistical analyses were made with STATISTICA, v. 6.0 (StatSoft, Tulsa, OK, USA) and R v. 3.0.1 (R Core Team, 2013); all of the means are given as the mean \pm SD. Significance levels were set at 0.05, and the two-tailed probability values are reported. Only 99 of 1134 distributions of the measured parameter values departed from normality (Kolmogorov-Smirnov test, $p > 0.05$). As parametrical ANOVA and discriminant analysis are relatively robust to departures from normality (Dillon and Goldstein, 1984), this was not an obstacle in the application of these tests.

We used a two-way ANOVA to test the influence of individuality and the inter-recording span on the call parameter values. For each ANOVA, factor individuality was represented by seven levels (individual European ground squirrels), factor inter-recording span was represented by two levels (preceding and subsequent recordings), and within each level calls were treated as replicates.

We used a discriminant function analysis with a jackknife confusion matrix (preDFA) to calculate the probability of classifying alarm calls to the correct individual for the preceding recordings of each data set (over-hours, over-days and over-year). For the jackknife procedure, each linear function was derived from all calls in the data set, except for the one being classified in a jackknifing cross-validation process (Manley, 1994). For each data set (over-hours, over-days, and over-year), we performed three preDFAs: 1) preDFA based on nine acoustic parameters measured from only the first element; 2) preDFA based on nine acoustic parameters measured from only the second element; and 3) preDFA based on nine acoustic parameters measured from both elements. The alarm calls containing both elements included a double set of acoustic parameters (nine from the first element and nine from the second element); therefore, we included in preDFA only the nine acoustic parameters that best contributed to discrimination based on Wilks' Lambda values. For the first element, we selected *dur1*, *f0 start1*, *f0 end1*, and *f0 center1*. For the second element, we selected *dur2*, *f0 start2*, *f0 end2*, *f0 center2* and *fbnd2*.

With the resulting pre/postDFAs, we classified alarm calls from the test sets (of the subsequent recordings) with discriminant functions derived from the training sets (of the preceding recordings), considering the value of the correct cross-validation as a measure of the retained individuality with time (Fig. 2; Klenova et al., 2011;

Matrosova et al., 2009, 2010a; Sibiryakova et al., 2015). We compared the values of correct assignment of alarm calls with a 2×2 Yates' chi-square test.

3. Results

A two-way ANOVA showed that the influence of individuality on call parameters was always stronger than the influence of the inter-recording span, for both the first element and the second element (Table 2). Individuality was encoded mainly in frequency parameters and less in temporal parameters.

When preDFAs were based on data sets from the preceding recordings and we used variables from the first element, the values of correct assignment to individuals were 93.7%, 91.8% and 93.0% for over-hours, over-days, and over-year data sets, respectively (Table 3). We obtained similar results when we used variables from the second element, with the values of correct assignment of 91.6%, 76.5%, and 93.0% for the over-hours, over-days, and over-year data sets, respectively. When we used nine acoustic parameters measured from both elements, the values of correct assignment increased to 96.8%, 97.7%, and 99.0% for over-hours, over-days and over-year data sets, respectively.

Pre/postDFAs applied to examine the retained individuality after some time span revealed a significant decrease of the correct assignment for all data sets, whether we used the first element, second element or both element variables (Table 3). Values of pre/postDFA correct assignment for the first element variables were 75.8%, 71.0%, and 47.8% for the over-hours, over-days, and over-year data sets, respectively. These assignments were significantly lower than the corresponding assignments from preDFAs based on the preceding recordings (over-hours: $\chi^2 = 10.42$, $p < 0.01$; over-days: $\chi^2 = 11.35$, $p < 0.001$; and over-year: $\chi^2 = 45.65$, $p < 0.001$; Fig. 3A). Values of pre/postDFA correct assignment for the second element variables were 60.4%, 65.0%, and 46.7% for the over-hours, over-days, and over-year data sets, respectively. These assignments were also significantly lower than the corresponding assignments from preDFAs for the over-hours ($\chi^2 = 23.26$, $p < 0.001$) and over-year data sets ($\chi^2 = 47.42$, $p < 0.001$), but not for the over-days data set ($\chi^2 = 2.37$, $p = 0.12$; Fig. 3B). When we used both element variables, we achieved pre/postDFA values of correct assignment of 83.5%, 87.0%, and 71.1% for the over-hours, over-days, and over-year data sets, respectively. These assignments were also significantly lower than the corresponding assignments from the preDFAs (over-hours: $\chi^2 = 8.11$, $p < 0.01$; over-days: $\chi^2 = 5.63$, $p < 0.05$; and over-year: $\chi^2 = 27.25$, $p < 0.001$; Fig. 3C). However, these were higher than when the variables from the first or second element were used singly.

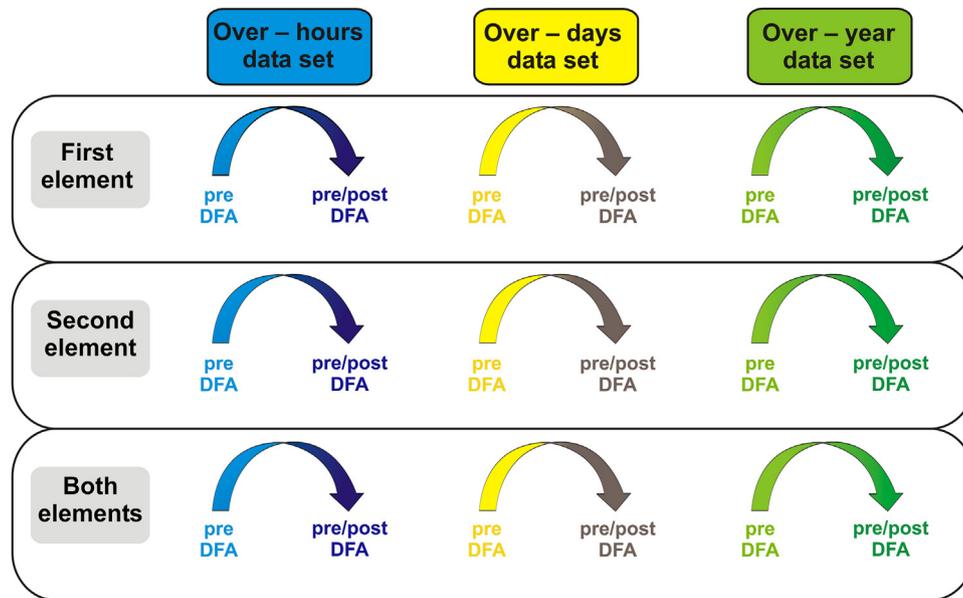


Fig. 2. Diagram showing discriminant function analyses performed in this study. For each data set, both preDFA and of pre/postDFA were performed separately for the first element, second element and for both elements. In preDFAs, sets of variables were derived from alarm calls recorded during the preceding recording. In pre/postDFAs, the training sets were derived from alarm calls recorded during the preceding recording, whereas testing sets were derived from alarm calls recorded during the subsequent recording made after a certain time span.

Table 2

Two-way ANOVA results for testing the influence of individuality and inter-recording span on acoustic variables of two alarm call elements in European ground squirrels; n – number of calls; *F* – *F*-ratio of ANOVA; *p* – significance level; and *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Call parameter	Inter-recording time span					
	Over-hours (n = 186)		Over-days (n = 185)		Over-year (n = 192)	
	Individuality	Time span	Individuality	Time span	Individuality	Time span
	$F_{6,178}$	$F_{1,178}$	$F_{6,177}$	$F_{1,177}$	$F_{6,184}$	$F_{1,184}$
First element						
<i>dur1</i>	89.66 ***	11.35 ***	98.26 ***	19.97 ***	54.59 ***	73.97 ***
<i>peak loc1</i>	13.72 ***	0.33, $p = 0.57$	4.82 ***	0.03, $p = 0.87$	6.48 ***	1.11, $p = 0.29$
<i>f0 start1</i>	275.1 ***	29.70 ***	309.8 ***	0.20, $p = 0.66$	231.9 ***	29.6 ***
<i>f0 end1</i>	320.5 ***	37.5, ***	391.1 ***	3.20, $p = 0.08$	294.1 ***	55.3 ***
<i>f0 center1</i>	384.5 ***	27.0, ***	535.8 ***	25.2 ***	313.1 ***	40.5 ***
<i>f0 maxamp1</i>	341.2 ***	22.6 ***	393.8 ***	3.10, $p = 0.08$	271.4 ***	36.2 ***
<i>f0 std1</i>	35.19 ***	0.98, $p = 0.32$	51.03 ***	6.75 *	21.42 ***	11.81 ***
<i>f0 mean1</i>	283.9 ***	14.9 ***	507.5 ***	12.1 ***	277.1 ***	21.5 ***
<i>fbnd1</i>	23.0 ***	0.08, $p = 0.77$	30.87 ***	5.07 *	13.59 ***	11.91 ***
Second element						
<i>dur2</i>	107.67 ***	1.86, $p = 0.17$	140.20 ***	2.89, $p = 0.09$	70.69 ***	0.06, $p = 0.82$
<i>peak loc2</i>	9.07 ***	8.24, **	10.21 ***	2.97, $p = 0.09$	11.96 ***	0.23, $p = 0.63$
<i>f0 start2</i>	151.94 ***	91.76 ***	114.2 ***	3.30, $p = 0.07$	156.92 ***	9.11 **
<i>f0 end2</i>	68.8 ***	116.6, ***	248.8 ***	15.4 ***	62.76 ***	20.51 ***
<i>f0 center2</i>	86.0 ***	203.3 ***	279.5 ***	16.6 ***	84.61 ***	8.20 **
<i>f0 maxamp2</i>	37.91 ***	85.84 ***	193.5 ***	14.57 ***	83.89 ***	0.18, $p = 0.67$
<i>f0 std2</i>	130.35 ***	8.39 **	56.14 ***	11.75 ***	121.91 ***	61.56 ***
<i>f0 mean2</i>	45.8 ***	103.3 ***	119.9 ***	2.27, $p = 0.12$	71.28 ***	2.43, $p = 0.12$
<i>fbnd2</i>	242.96 ***	0.98, $p = 0.32$	78.45 ***	2.80, $p = 0.10$	169.06 ***	49.86 ***

The pre/postDFA correct assignment values were always lowest for the over-year data sets (Table 3; Fig. 3). When we used first element variables, we found that pre/postDFA correct assignments significantly decreased with a time span of over-year in comparison with a time span of over-hours ($\chi^2 = 14.02$, $p < 0.001$) and a time span of over-days ($\chi^2 = 9.77$, $p < 0.01$). When we used second element variables, we found that pre/postDFA correct assignments significantly decreased with the over-year time span in comparison with the over-days time span ($\chi^2 = 5.77$, $p < 0.05$) and marginally significantly decreased in comparison with the over-hours time span ($\chi^2 = 2.92$, $p = 0.09$). When we used both element variables, pre/postDFA correct assignments decreased significantly with the

over-year time span in comparison with the over-days time span ($\chi^2 = 5.98$, $p < 0.05$) but only marginally so in comparison to the over-hours time span ($\chi^2 = 3.00$, $p = 0.08$) (Fig. 3).

The use of both elements always resulted in a better retention of individuality compared to the first element singly, although significant results were achieved only in cases of the over-days data set ($\chi^2 = 6.78$, $p < 0.01$) and the over-year data set ($\chi^2 = 9.97$, $p < 0.01$) (Fig. 3). Both elements resulted in a better retention of individuality compared to the second element singly in all cases: over-hours data set ($\chi^2 = 10.90$, $p < 0.01$), over-days data set ($\chi^2 = 12.09$, $p < 0.001$), and over-year data set ($\chi^2 = 10.89$, $p < 0.01$) (Table 3; Fig. 3).

Table 3
Results of discriminant function analyses (preDFAs) and cross-validation procedures (pre/postDFAs). Values of correct assignment (in percents) are given for over-hours, over-days and over-year data sets for each individual and separately for the first element, for the second element and for both elements.

	Individual	First element		Second element		Both elements	
		preDFA	pre/postDFA	preDFA	pre/postDFA	preDFA	pre/postDFA
Over-hours							
	F34888	100.0	100.0	100.0	80.0	100.0	93.3
	F46191	81.8	90.0	90.9	20.0	81.8	50.0
	F418044	100.0	86.7	100.0	26.7	100.0	100.0
	F854982	100.0	60.0	92.3	100.0	100.0	100.0
	M845415	100.0	0.0	80.0	0.0	100.0	18.2
	F34237	80.0	86.7	80.0	86.7	93.3	100.0
	M418114	92.3	86.7	100.0	93.3	100.0	100.0
	Total	93.7	75.8	91.6	60.4	96.8	83.5
Over-days							
	F418044	70.0	0.0	90.0	46.7	100.0	100.0
	F420663	83.3	100.0	33.3	80.0	100.0	86.7
	F34567	100.0	100.0	81.8	70.0	100.0	100.0
	F854982	80.0	93.3	30.0	26.7	80.0	100.0
	M845415	100.0	100.0	83.3	73.3	100.0	100.0
	F31605	100.0	93.3	100.0	93.3	100.0	100.0
	F848552	100.0	20.0	100.0	66.7	100.0	26.7
	Total	91.8	71.0	76.5	65.0	97.6	87.0
Over-year							
	F34888	100.0	6.7	86.7	33.3	100.0	53.3
	F95186	90.0	0.0	100.0	16.7	90.0	16.7
	F46191	93.3	85.7	80.0	78.6	100.0	100.0
	F34567	100.0	100.0	100.0	70.0	100.0	100.0
	F418044	100.0	0.0	93.3	0.0	100.0	18.2
	F420663	80.0	40.0	100.0	100.0	100.0	100.0
	F848552	86.7	100.0	93.3	20.0	100.0	100.0
	Total	93.0	47.8	93.0	46.7	99.0	71.7

4. Discussion

We found that vocal individuality in the alarm calls of the European ground squirrel was similarly high and did not differ when we used variables from only the first element, from only the second element or from both elements. Vocal individuality decreased with time, even over short time spans of a few hours. This applied to variables of any call element or both call elements. Vocal individuality decreased with the increased time span between repeated recordings, and this decrease was stronger for the over-year time span than for the over-days or over-hours time spans. Call stability was best achieved with variables from both elements, worse with variables from only the first element and worst with variables from only the second element.

Our study confirmed the conclusions of previous studies (Schneiderová and Policht, 2010; Schneiderová, 2012) that from a short-term perspective, the alarm calls of the European ground squirrel have a strong potential to encode individual differences and allow the discrimination of individual callers. In this regard, both elements that comprised the alarm calls provided strong cues to individuality. The acoustic parameters measured from either the first or the second element were already sufficient for a nearly 100% reliable discrimination of individual callers. The frequency modulation pattern of the second element displayed considerable among-individual variability (see Supplementary Material), which may reflect its significant role as an individual signature. However, Schneiderová (2012) demonstrated that the second element also had high within-individual variability, even for calls coming from a single recording session, which reduced its usefulness for individual discrimination compared to the more consistent first element. The present study additionally confirmed that adding the second element did not improve the extent to which calls could be classified to correct individuals beyond that based on the first element alone (Schneiderová, 2012). Therefore, simply combining both elements did not enhance the discriminating power if the alarm calls

were recorded within only one (in this case preceding) recording session per individual.

In the present study, we re-recorded several permanently marked European ground squirrels over different time spans (hours, days, and year), and we estimated the percentage of calls correctly classified to individuals when using calls from preceding recordings as the training set and calls from subsequent recordings as the testing set. This approach allowed us to evaluate the effect of combining both elements from a long-term perspective. We found that variables from both elements were much more effective for maintaining individually recognizable calls for longer periods than variables from any single element. Individually distinctive frequency modulation patterns were recognizable, even after one year in some animals (see Supplementary Material).

In general, alarm calls of ground squirrels contain poor cues of sex or age (Matrosova et al., 2007, 2011, 2012; Swan and Hare, 2008; Volodina et al., 2010), but salient cues of individual identity (Hare, 1998; McCowan and Hooper, 2002; Volodin, 2005; Matrosova et al., 2009, 2010a, 2010b, 2011). One of the most relevant hypotheses for the adaptive utility of strong individuality encoded in alarm calls of ground-dwelling sciurids is the “caller reliability hypothesis” (Hare and Atkins, 2001; Blumstein et al., 2004). It was demonstrated that some ground-dwelling sciurids selectively responded towards calls of experienced (reliable) versus inexperienced (unreliable) callers. By ignoring false threats, they avoided wasting time that could be devoted to foraging. However, the “caller reliability hypothesis” has been challenged by studies demonstrating the temporal instability of alarm calls (Matrosova et al., 2009, 2010a,b) because individual callers can be recognized by conspecifics as reliable or unreliable only if their alarm calls retain individualistic traits over time.

Previous studies with speckled and yellow ground squirrels showed that the vocal individuality of alarm calls was very unstable over time (Matrosova et al., 2009, 2010a,b). However, these studies examined either single-element calls, in the case of the speckled ground squirrel (Matrosova et al., 2009), or selected single elements of multi-element calls, in the case of the yellow ground squirrel

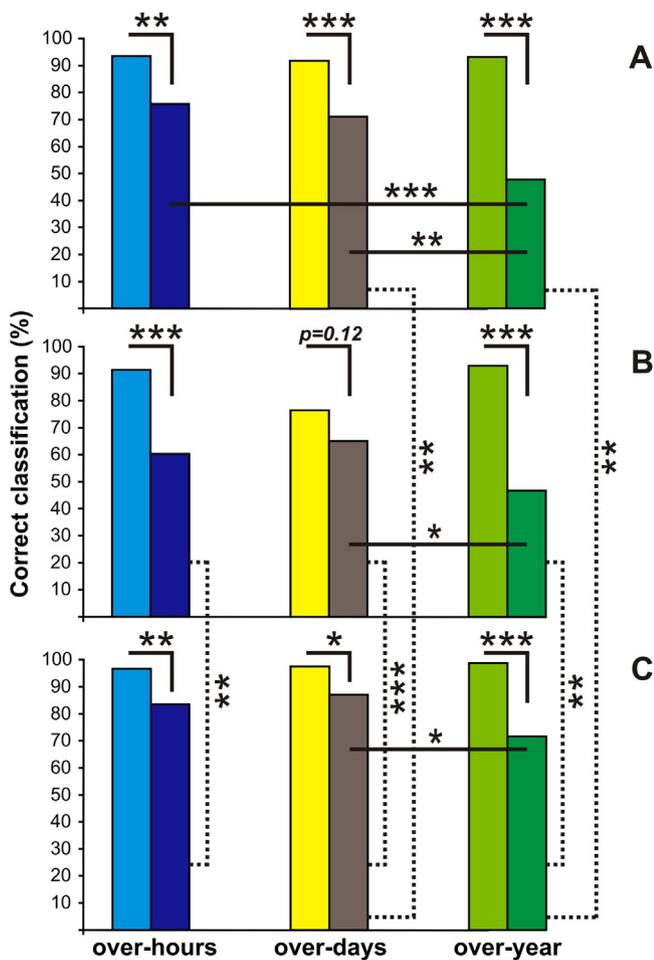


Fig. 3. Results of preDFAs (on preceding recordings, left bars) and of pre/postDFAs (when alarm calls from the test sets of the subsequent recordings classified with discriminant functions derived from the training sets of the preceding recordings, right bars) showing the retained individuality after three different time spans (over-hours, over-days, and over-year) for the alarm call first element (A), second element (B) and for both elements (C). Comparisons of correct assignment values between preDFA and pre/postDFA with χ^2 tests are shown by the right angle lines. Comparisons between different pre/postDFAs with χ^2 tests are shown by horizontal lines and by vertical brackets. Only significant differences are presented; *** $p < 0.001$; ** $p < 0.01$; and * $p < 0.05$.

(Matrosova et al., 2010a,b). The present study is the first in which two structurally different call elements together were examined for their stability in any ground squirrel species. The stability over time for multi-element acoustic signals has been documented for common marmosets (*Callithrix jacchus*; Jones et al., 1993), northern elephant seals (*Mirounga angustirostris*; Casey et al., 2015) and some bird species (Klenova et al., 2009; Humphries et al., 2016).

Our results reveal that creating a binary alarm call by adding only one element is sufficient to increase the stability of individual traits, even over longer periods of time (over year). Therefore, calls containing more elements or syllables are potentially more appropriate for maintaining individual identity over time. These results supported the “caller reliability hypothesis” for species of ground squirrels that produce multiple-note alarm calls, e.g., the Richardson’s ground squirrel (*S. richardsonii*), for which the “caller reliability hypothesis” was proposed (Hare and Atkins, 2001). However, these data did not support the “caller reliability hypothesis” for ground squirrel species that produced only single-element alarm calls, e.g., the speckled ground squirrel (Matrosova et al., 2009).

Clarification of the adaptive significance of retaining and recognizing individually-distinct alarm calls should not be detached from our concurrently increasing knowledge of learning and memory in obligatory hibernating ground-dwelling sciurids. There would be no reason to expect that European ground squirrels retain and recognize their individually-distinct alarm calls for long term periods (such as one year) if hibernation significantly altered their social memory. Belding’s ground squirrels (*S. beldingi*) recognized odours of littermates and previously familiar nonlittermates after hibernation, although their recognition of familiar and unfamiliar odours seemed to be suppressed (Mateo and Johnston, 2000). Millesi et al. (2001) demonstrated, with a nest-sharing preference test, that the social memory was unaffected by hibernation in European ground squirrels, although these experiments were also based on olfactory and visual stimuli, not acoustic stimuli.

Second frequency modulated elements may represent an interesting adaptation in the alarm calls of ground-dwelling sciurids. These elements were described for five Eurasian ground squirrels (Nikol’skii, 1979; Schneiderová and Policht, 2012) and two North American ground squirrels, the California ground squirrel (*S. beecheyi*; Leger and Owings, 1978) and the Richardson’s ground squirrel (*S. richardsonii*; Sloan et al., 2005). In these North American species, the second elements were not included in all of the alarm calls, and playback experiments highlighted their function in risk evaluation and localization (Leger and Owings, 1978; Sloan et al., 2005). The present study points to the additional importance of the second elements for the long-term discrimination of individual signalers. Playback experiments investigating the functional significance of the second frequency modulated elements have never been conducted in any Eurasian ground squirrel. Therefore, apart from testing whether they also reflect the degree of perceived risk and enhance the localizability of callers, it would be useful to investigate whether their inclusion indeed enhances individual recognition by conspecifics. In some mammals and birds, playback experiments have revealed that the frequency modulation plays a crucial role in individual recognition (Charrier et al., 2001, 2002, 2009; Lengagne et al., 2001). The inclusion of frequency modulated elements also appears to be challenging from the ontogenetic point of view. A pilot study of the alarm calls of captive juvenile European ground squirrels indicated that juveniles newly emerged from burrows did not utter the second frequency modulated element and that this element emerged during subsequent development (Schneiderová et al., 2015).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.beproc.2017.02.014>.

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