Between-year stability of individual alarm calls in the yellow ground squirrel *Spermophilus fulvus*

Vera A. Matrosova, Ilya A. Volodin,* Elena V. Volodina, Nina A. Vasilieva, and Alexandra A. Kochetkova

Department of Vertebrate Zoology, Faculty of Biology, Lomonosov Moscow State University, Vorobievy Gory 1/12, Moscow, 119991, Russia (VAM, IAV, AAK)
Scientific Research Department, Moscow Zoo, B. Gruzinskaya, 1, Moscow, 123242, Russia (IAV, EVV)
Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Leninsky pr., 33, Moscow, 119071, Russia (NAV)

* Correspondent: volodinsvoc@gmail.com

Although individuality in alarm calls has been reported for many ground-dwelling sciurids, the degree to which the vocal identity encoded in alarm calls is stable with time has been studied only for a single sciurid species. Thus, no comparable data are available. We examined the retention of the vocal keys to individual identity after hibernation in a natural colony of yellow ground squirrels (*Spermophilus fulvus*), long-lived, obligate-hibernating rodents that maintain stable social groups for years. We recorded alarm calls in 2 subsequent years, separated by hibernation, from 22 individually marked animals. All individuals could be distinguished with high probability by their alarm calls within a year. However, only 6 of the 22 animals kept their alarm calls stable after hibernation. Sex, age, year of data collection, and the distance that individuals moved between years did not have significant effects on the retention of a stable alarm call structure after hibernation. Given the low proportion of individuals with stable alarm calls, vocal identity cannot be the only modality sufficient to secure the recovery of personalized social relationships after hibernation in the yellow ground squirrel. DOI: 10.1644/09-MAMM-A-143.1.

Key words: alarm call, rodent, *Spermophilus fulvus*, temporal stability, vocal communication, yellow ground squirrel

Individually distinctive long-range calls have been found in many mammals (Fischer et al. 2001; McComb et al. 2003; Randall et al. 2005; Tooze et al. 1990; Volodina et al. 2006; Yin and McCowan 2004), and playback experiments, conducted with both natural and artificially modified vocalizations, showed that animals recognize their conspecifics individually by voice (Charrier et al. 2002; Frommolt et al. 2003; Poole 1999; but see Schibler and Manser 2007). Ground-dwelling sciurids represent a convenient model for studying the role of individual identity encoded in the alarm call (Blumstein 2007), which has been tested for steppe marmots (*Marmota bobak*—Nikol'skii and Suchanova 1994), yellow-bellied marmots (*M. flaviventris*—Blumstein and Munos 2005), Belding's ground squirrels (*Spermophilus beldingi*—Leger et al. 1984; McCowan and Hooper 2002), and speckled ground squirrels (*S. suslicus*—Matrosova et al. 2009; Volodin 2005). In Richardson's ground squirrels (*S. richardsonii*) and yellow-bellied marmots the ability to recognize played back alarm calls of different individuals has been shown (Blumstein and Daniel 2004; Blumstein et al. 2004; Hare 1998; Hare and Atkins 2001). Thus, individually

distinctive alarm calls can help to maintain personalized relations in local groups of ground-dwelling sciurids (Blumstein 2007; Manno et al. 2007; Sherman 1977).

Most ground squirrel species live in regions with continental climates and are obligate hibernators during seasons with low ambient temperatures and poor foraging conditions (Armitage 1981). Animals that emerge from hibernation should reestablish the social relationships that they had with their mates, rivals, and kin in the previous year, and retaining their individual alarm calls is likely to help them do this.

Previously we showed that some individual speckled ground squirrels retain after hibernation the keys to identity encoded in the structure of their alarm calls (Matrosova et al. 2009). Consistent with acoustic data, experiments have shown that olfactory stimuli also retain the keys to identity after hibernation in Belding's and European ground squirrels (*S. citellus*—Mateo and Johnston 2000; Millesi et al. 2001).

The object species of this study, the yellow ground squirrel (*S. fulvus*), is a relatively long-living (up to 7 years—A. V. Tchabovsky, Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, pers. comm.), diurnal, herbivorous, obligatory-hibernating sciurid (Efimov 2005; Ismagilov 1969). This is the largest of the *Spermophilus* species, with a body length without tail of 230–370 mm, a body mass at emergence from the hibernation of 600–900 g, and a body mass before hibernation of 1,600–2,000 g (Efimov 2005; Ismagilov 1969; Matrosova et al. 2007). Female yearlings are capable of breeding after their 1st hibernation, and males after their 2nd one (Efimov 2005; Popov et al. 2006). Yellow ground squirrels inhabit open steppe and desert habitats with rarefied grasses and tend to locate their burrows on local relief elevations (Ismagilov 1969; Kashkarov and Lein 1927). Taken together with the large size of these animals, the preferred habitat and burrow location of this species provides them with a good survey, allowing group members to see each other, and favors the advanced sociality of this species compared to the smaller *Spermophilus* (Tchabovsky 2005). Sociality in the yellow ground squirrel is evident from the male hierarchy during the mating period (Bokshtein et al. 1989), from social play that occurs between littermates, and from affiliative mother–offspring contacts, occurring up to hibernation (Stukolova et al. 2006). Many female yellow ground squirrels hold the same home territories for years, resulting in stable local groups (Shilova et al. 2006). Average distances between the centers of neighboring home territories vary from 49 to 108 m depending on population density, and home territories overlap widely (Popov 2007; Shilova et al. 2006). This enables yellow ground squirrels to hear the alarm calls of neighbors and respond to them. Given these aspects of the biology of the yellow ground squirrel, we expected that their individual alarm calls, which ensure personalized relations between group members during above-ground activity and after hibernation, should be relatively stable with time and after hibernation.

The alarm call is the loudest and most common call type used by yellow ground squirrels. Its structure is the same in all predatory contexts: toward raptors, terrestrial predators, some harmless animals (e.g., hares), and humans (Nikol'skii 1979). The alarm call consists of tonal notes with a maximum fundamental frequency of 5,000–6,000 Hz, a depth of frequency modulation of 2,500–3,000 Hz, and a note duration of about 70 ms, emitted in clusters of 2–16 notes. These clusters can occur singly or be produced repetitively, resulting in series, with intercluster intervals substantially longer than cluster duration (Nikol'skii 1979; Titov et al. 2005). Unusual for mammals, the fundamental frequency of the alarm call is slightly but significantly lower in pups than it is in adults, although the adults are much larger in size and body mass (Matrosova et al. 2007). The purposes of this study were to describe in further detail the alarm call structure of the yellow ground squirrel, to examine whether individuals have distinctive alarm calls, and to investigate whether the individually specific alarm call structure retains stable in the same individuals after hibernation.

MATERIALS AND METHODS

Subjects and study area.—We recorded alarm calls from 22 (5 male and 17 female) adult (1 year old and older) yellow ground squirrels during brief capture–recaptures in their natural colony in Saratov Province, Russia, near the Djakovka settlement (50°43′88″N, 46°46′04″E). Each individual was recorded 1 or a few times from mid-May to mid-June in 2 successive years, 2005–2006 (19 animals) or 2006–2007 (3 animals).

The study grid of 31.6 ha represents a part of hemipsammophite steppe, which is under permanent grazing pressure from domestic cattle. The height of grass in June is 5–20 cm, and the projective cover ranges from 20% to 80% (Shilova et al. 2006). Aboveground activity of the study colony lasts 4–5 months annually, from early to mid-March until early to mid-August, depending on the year (Popov 2007).

Spatial coordinates of animals.—This colony has been used for a long-term study of behavioral ecology since 2001 (Popov 2007; Shilova et al. 2006). Before this study all the animals on the study grid were captured and individually marked with both microchips (Bayer AG, Leverhusen, Germany) and dye marks (urzol black D for fur, *p*-phenylenediamine; Rhodia, Paris, France). For capturing, loops or $80 \times 80 \times 80$-cm wire-mesh live traps of original construction without bait were used. This live trap has no top, and it has a falling door in the bottom. For capturing, the live trap is placed onto the entrance of a burrow from above and the door is opened and set so that it falls when an animal emerges from its burrow. During this study each animal was captured twice and placed singly into a $30 \times 15 \times 15$-cm wire-mesh hutch for a subsequent acoustic recording.

Spatial coordinates for points of captures and visual registrations of dye-marked subjects were collected with a global positioning system navigator (Garmin 12; Garmin Ltd., Olathe, Kansas). With ArcView 3.3 software (ESRI Inc., Redlands, California) we calculated the average spatial coordinates for each subject during May–June for each study year (1–31 points per animal; $\bar{X} = 10.5 \pm 7.5$ *SD*). We used these coordinates to calculate the distance individuals moved between years, separated by their hibernation. This distance was taken as a measure of constancy of social environment after hibernation for the given animal.

Call recording procedure and equipment.—All acoustic recordings were made within 1 h of capture from animals sitting in hutches. From the hutch, animals emitted calls toward a human observer, sitting within 2 m, either spontaneously or in response to additional stimulation (movements of a handheld baseball cap). All stimulation stopped as soon as an animal started calling. On average, a recording session lasted 3–4 min and provided 30–40 alarm call clusters per animal. Distance to the microphone was about 1 m. In live traps the pattern of calling toward humans and the structure of alarm calls were similar to the patterns that occurred under natural conditions toward predators (Matrosova et al. 2007; Nikol'skii 1979) allowing us to distinguish reliably these calls as alarms. The sound recording session always preceded any

TABLE 1.—Measured alarm call parameters and the parameter values (mean $\pm$ *SD*, minimum–maximum) for 22 yellow ground squirrels (*Spermophilus fulvus*). $n = 425$ alarm call clusters.

Call parameter	Parameter description	Parameter statistics	
		$\bar{X} \pm SD$	Minimum–maximum
f st[a]	Fundamental frequency at the start of a 2nd note in a cluster (kHz)	2.45 ± 0.45	1.47–4.99
f max[a]	Maximum fundamental frequency of a 2nd note in a cluster (kHz)	5.47 ± 0.42	4.31–6.39
f end[a]	Fundamental frequency at the end of a 2nd note in a cluster (kHz)	1.93 ± 0.18	1.42–2.78
freq mod	Difference between the f max and the least of f st and f end values (kHz)	3.54 ± 0.42	2.35–4.55
dur st-max[a]	Time period from the beginning of a 2nd note in a cluster to the point of maximum fundamental frequency of a note (ms)	43 ± 8	28–69
dur max-end[a]	Time period from the point of maximum fundamental frequency to the end of a 2nd note in a cluster (ms)	18 ± 3	10–26
dur note	Duration of a 2nd note in a cluster (ms)	61 ± 8	42–89
quart 1[a]	Value of the 1st energy quartile of a 2nd note in a cluster (kHz)	3.79 ± 0.41	2.69–5.10
period 1–2[a]	Time period from the start of a 1st note to the start of a 2nd note in a cluster (ms)	209 ± 31	136–331
df max 1–2[a]	Difference between the maximum fundamental frequencies of a 1st and of a 2nd note in a cluster (kHz)	-0.11 ± 0.21	-0.75–0.66
n notes	Number of notes in a cluster	3.9 ± 1.4	2–8

[a] Parameters included in DFA.

other manipulations with an animal (checking individual marks and determining age and sex). After manipulations animals were released at the point of capture. All 22 study animals were familiar with capture and call-recording procedures before the start of this study. All methods followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

For recordings we used a Marantz PMD-222 analog tape recorder (D&M Professional, Kanagawa, Japan) with AKG-C1000S cardioid electret condenser microphone (AKG-Acoustics Gmbh, Vienna, Austria), and Type II chrome audiocassette EMTEC-CS II (EMTEC Consumer Media, Ludwigshafen, Germany). We also used a Marantz PMD-671 CF-recorder with Sennheiser K6 ME-64 cardioid electret condenser microphone (Sennheiser Electronic, Wedemark, Germany). These systems provided a qualitative recording within ranges 40–14,000 Hz and 40–24,000 Hz, respectively. For the spectrographic analysis we used Avisoft SASLab Pro software version 4.3 (Avisoft Bioacoustics, Berlin, Germany). 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, fast Fourier transform length 1,024 points, frame 50%, and overlap 96.87%. These settings provided a bandwidth of 61 Hz, a frequency resolution of 23 Hz, and a time resolution of 1.3 ms.

Call analysis.—We recorded each of the 22 study animals twice. For each animal, the recordings were separated by hibernation ($\bar{X} = 365.1$ days ± 14.9 *SD*), hereafter ''1st year'' and ''2nd year'' recording, respectively, for 44 recordings in total. From each recording we took measurements from 10 randomly selected alarm call clusters of good quality and high amplitude that were not disrupted by wind (4 recordings provided only 3–7 clusters). In total, we analyzed 425 clusters, 213 clusters for the 1st year recordings and 212 clusters for the 2nd year recordings. All 425 clusters from the 22 study animals were used for a quantitative description of yellow ground squirrel alarm call structure.

For the quantitative description of the yellow ground squirrel alarm call we used measurements of 8 note parameters and 3 cluster parameters (Table 1; Fig. 1). These parameters were selected as the least correlated of 18 parameters on the basis of the preceding principal component analysis. All measurements were exported automatically to Microsoft Excel (Microsoft Corp., Redmond, Washington). Because the 1st note in a cluster is usually slightly more distinctive in appearance from all subsequent notes, which are very similar
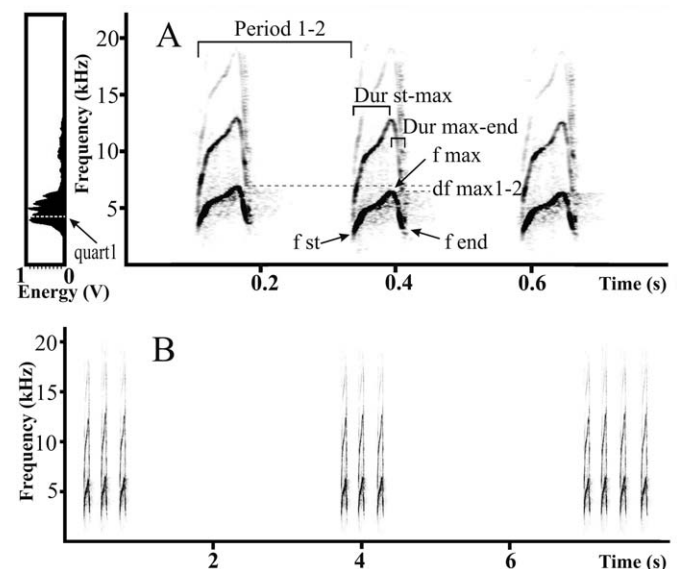

FIG. 1.—Alarm calls of the yellow ground squirrel (*Spermophilus fulvus*) and measurements taken from alarm call notes and clusters of the yellow ground squirrel (see Table 1 for description of parameters). A) Enlarged view of 1st cluster from the series in B. B) Part of a natural series of 3 alarm call clusters produced by an individual yellow ground squirrel.

to each other, we took all the note parameters from the 2nd note in each cluster. From the screen with the reticule cursor we measured the following note parameters: 4 fundamental frequency parameters, 3 duration parameters, and 1 power spectrum parameter (Table 1; Fig. 1). For each cluster we calculated the number of notes, measured the time period from the start of a 1st to the start of a 2nd note, and calculated the difference between maximum fundamental frequencies of a 1st and a 2nd note (Table 1; Fig. 1). We did not measure the interval between alarm call clusters because this parameter could be influenced by the behavior of the observer.

Statistical analyses.—We used a 2-way multivariate analysis of variance (MANOVA) to test the influence of individuality and year of recording on the values of the call parameters. The 2-way MANOVA could be used here because a Kolmogorov–Smirnov test showed that distributions of parameter values differed from normality ($P < 0.05$) only in 6 (2.48%) of 242 comparisons. The parameter n notes differed from normality in 3 animals, and f st, f end, and df max 1–2 each in 1 animal. We used a repeated-measures analysis of variance (ANOVA) to compare the individual mean parameter values for calls of 1st-year and 2nd-year recordings. The repeated-measures ANOVA could be used here because a Kolmogorov–Smirnov test showed that distributions of parameter values did not differ from normality ($P > 0.20$) in all 22 comparisons. We used a Mann–Whitney U-test and a Fisher exact test to estimate the effects of age, sex, year, and distance that individuals moved between years in stable and unstable callers.

We used discriminant function analysis (DFA) to calculate the probability of the correct assignment of alarm calls to the correct individual for each call sample (of 1st-year and 2nd-year recordings). We included into DFA 8 of the 11 measured alarm call parameters (Table 1), excluding frequency modulation (freq mod) and note duration (dur note), which were derived from other parameters, and also the number of notes (n notes), distribution of which often differed from normality. We classified calls from the test sets (of 2nd year) with DFA functions derived from the training call set (of 1st year), considering the value of the correct cross-validation as a measure of the retention of individuality with time (Klenova et al. 2009; Matrosova et al. 2009; Tripp and Otter 2006).

We calculated the expected level of correct classification with DFA if the calls we analyzed were distributed randomly among individuals (Solow 1990). To perform the randomization analysis 500 permutation procedures with macros, specially created for STATISTICA software, were used. Each permutation procedure included the random permutation of 213 calls (for the 1st-year recordings) or 212 calls (for the 2nd-year recordings) among 22 randomization groups, according to the number of animals examined and followed by DFA standard procedure. We then created the distribution of mean classification percentages to randomization groups and estimated a position of the observed value of assignment to pairs within this distribution. If the observed value exceeded 95% of values within this distribution, we established that the

TABLE 2.—Two-way MANOVA results for the individuality and year of recording effects on the alarm call parameter values in 22 yellow ground squirrels (*Spermophilus fulvus*). F = F-ratio of MANOVA; P = significance level.

Call parameter	Individuality effect		Year of recording effect	
	$F_{21,402}$	P	$F_{1,402}$	P
f st	60.61	<0.001	47.01	<0.001
f max	52.62	<0.001	64.38	<0.001
f end	11.37	<0.001	13.51	<0.001
freq mod	42.38	<0.001	25.66	<0.001
dur st-max	56.21	<0.001	21.77	<0.001
dur max-end	14.42	<0.001	19.87	<0.001
dur note	47.92	<0.001	4.07	<0.05
quart 1	26.85	<0.001	153.77	<0.001
period 1–2	37.18	<0.001	14.20	<0.001
df max 1–2	18.88	<0.001	5.63	<0.05
n notes	11.83	<0.001	11.99	<0.001

observed value did differ significantly from the random one with $P < 0.05$. If the observed value exceeded 99% of values within this distribution, we established that the observed value did differ significantly from the random one with $P < 0.01$ (Klenova et al. 2008; Solow 1990).

All statistical analyses were made with STATISTICA, version 6.0 (StatSoft, Tulsa, Oklahoma). All tests were 2-tailed, and differences were considered significant where $P < 0.05$.

RESULTS

Alarm calls of the yellow ground squirrel represent clusters of short notes modulated in frequency (Table 1). The modulation is deeply inverted U-shaped, with the position of maximum fundamental frequency skewed to the end of a note. In 68.2% (290 of 425) analyzed clusters, the maximum fundamental frequency of a 2nd note was lower than those of a 1st note, in 18.4% (78 of 425) clusters it was higher, and only in 13.4% (57 of 425) clusters of the same frequency. The fundamental frequency always had the highest energy relative to the harmonics, thus, the maximum intensity frequency was located within a fundamental frequency band.

The MANOVA showed that the effects of factors individuality and year of recording on the alarm call parameter values were significant for all the 11 alarm call parameters (Table 2). Comparison of F-ratios from the MANOVA indicated that the variability in call parameter values among individuals was comparable to that between years. Despite the significant effect by year of recording, values for only 3 (f st, f max, and quart 1) of the 11 alarm call parameters increased after hibernation (Table 3). The values of remaining 8 parameters did not differ by year.

The DFA conducted with alarm calls of the 1st-year recordings showed 94.4% correct assignment of calls to individual (Table 4), which significantly exceeds the random value (18.1%) calculated with the randomization procedure ($P < 0.001$). For alarm calls of the 2nd-year recordings DFA

TABLE 3.—Repeated-measures ANOVA results for the year of recording effect on the mean alarm call parameter values in 22 yellow ground squirrels (*Spermophilus fulvus*). $F = F$-ratio of ANOVA; $P =$ significance level.

| Call parameter | $\bar{X} \pm SD$ values | | Year of recording effect | |
	1st year	2nd year	$F_{1,21}$	P
f st (kHz)	2.36 ± 0.38	2.51 ± 0.46	6.07	<0.05
f max (kHz)	5.40 ± 0.36	5.55 ± 0.42	4.53	<0.05
f end (kHz)	1.90 ± 0.13	1.95 ± 0.17	1.56	0.225
freq mod (kHz)	3.50 ± 0.39	3.60 ± 0.38	1.88	0.184
dur st-max (ms)	44 ± 8	42 ± 6	2.95	0.101
dur max-end (ms)	17 ± 2	18 ± 3	1.87	0.186
dur note (ms)	61 ± 8	60 ± 8	0.64	0.434
quart 1 (kHz)	3.64 ± 0.43	3.94 ± 0.24	13.12	<0.01
period 1–2 (ms)	212 ± 31	205 ± 26	1.30	0.267
df max 1–2 (kHz)	0.08 ± 0.13	0.11 ± 0.21	1.03	0.321
n notes	3.7 ± 0.9	4.0 ± 1.1	2.42	0.135

showed similarly high percentage of correct assignment to individual (94.8%, random value 17.9%; $P < 0.001$). Cross-validation of alarm calls from the test set (alarm calls of the 2nd-year recordings) with discriminant functions derived from the training set (alarm calls of the 1st-year recordings) showed a decline of correct assignment to individual of as little as 29.2% (Table 4). Nevertheless, some degree of individuality

TABLE 4.—Percentages of alarm calls correctly classified to individual with discriminant function analysis (DFA) and the results of cross-validation for alarm calls, recorded from each of 22 yellow ground squirrels (*Spermophilus fulvus*) over a year (after hibernation). $n =$ number of alarm calls.

| Individual | 1st-year DFA | | 2nd-year DFA | | Cross-validation | |
	n	%	n	%	n	%
Male 43	7	100	3	66.7	3	0
Female 50	10	100	10	100	10	0
Female 64	10	90	10	100	10	30
Male 92	10	100	10	80	10	0
Male 107	10	100	10	100	10	100
Female 148	10	100	10	100	10	0
Female 154	10	90	10	100	10	0
Female 208	10	100	10	90	10	0
Female 210	6	66.7	10	100	10	90
Female 216	10	90	10	60	10	50
Female 225	10	100	10	100	10	30
Female 265	10	100	10	100	10	60
Female 271	10	100	10	100	10	20
Male 284	10	100	10	100	10	10
Female 291	10	90	10	90	10	0
Female 329	10	100	10	100	10	100
Female 379	10	100	9	88.9	9	22.2
Female 385	10	90	10	100	10	10
Female 397	10	90	10	100	10	90
Male 416	10	70	10	100	10	0
Female 1081	10	90	10	100	10	0
Female 1128	10	100	10	90	10	10
Total	213	94.4	212	94.8	212	29.2

TABLE 5.—Percentages of correct classification of alarm calls to individual with discriminant function analysis (DFA) and cross-validation results for alarm calls, recorded after hibernation, for subsets of the 6 stable callers and 6 unstable callers. $n =$ number of alarm calls.

| Individual | 1st-year DFA | | 2nd-year DFA | | Cross-validation | |
	n	%	n	%	n	%
Stable callers						
Male 107	10	100	10	100	10	100
Female 210	6	83.3	10	100	10	90
Female 216	10	100	10	100	10	50
Female 265	10	100	10	100	10	100
Female 329	10	100	10	100	10	100
Female 397	10	100	10	100	10	100
Total	56	98.2	60	100	60	90
Unstable callers						
Female 50	10	100	10	100	10	0
Female 148	10	100	10	100	10	30
Female 154	10	100	10	100	10	50
Female 208	10	100	10	100	10	30
Male 416	10	100	10	100	10	0
Female 1081	10	100	10	100	10	10
Total	60	100	60	100	60	20

was retained in calls because even over a year the percentages of correctly classified calls exceeded the random value. Alarm calls could be distinguished from total call sample with a high probability (not below 50%) for only 27% (6 of 22) of the yellow ground squirrels (1 male and 5 females). In the remaining 16 individuals call structures changed substantially over a year and were not distinguishable from total call sample (Table 4).

We made further DFA and cross-validation separately for 2 subsets, with 6 animals in each (Table 5). The 1st subset included calls from the 6 animals that showed the best cross-validation values (not below 50%), called hereafter ''stable callers.'' The 2nd subset included calls from 6 animals (1 male and 5 females), selected randomly from the 10 animals, that showed the worst (0) cross-validation values, called hereafter ''unstable callers.''

For both stable and unstable callers and 1st-year and 2nd-year recordings, DFA showed similarly high total percentages (98.2–100%) of correct assignment of alarm calls to individual (Table 5). However, the between-year cross-validation was very high (90%) for the stable callers and very low (20%) for the unstable callers.

We estimated the influence of different factors on the retention of stability of the individual alarm call structure after hibernation. Neither age ($U = 42.5$, $n_1 = 6$, $n_2 = 16$; $P = 0.69$), nor sex (Fisher exact test, $P = 1.0$), nor year of data collection (Fisher exact test, $P = 1.0$) showed significant effects on the retention of a stable alarm call structure. Similarly, the mean distance that individuals moved between years did not differ significantly between stable callers ($\bar{X} = 32.6$ m ± 37.6 SD, $n = 6$) and unstable callers ($\bar{X} = 55.2 ± 45.2$ m, $n = 16$; $U = 31$, $P = 0.21$).

DISCUSSION

The alarm calls of individual yellow ground squirrels were very similar within a recording session, providing very high individual distinctiveness. After hibernation only 27% (6 of 22) of the study animals kept the structure of their alarm calls stable, and the remaining 16 animals changed it strongly. We observed no significant effect of sex, age, or constancy of social environment on whether a particular animal kept the structure of its alarm calls stable or changed it after hibernation.

To examine individuality we took calls from 1 recording per animal before hibernation and 1 recording after hibernation, because in nature ground squirrels should recognize individuals when they produce a single alarm call series within a single predatory event. High individuality of the alarm call structure within a single recording session also has been reported for Belding's ground squirrels (McCowan and Hooper 2002) and speckled ground squirrels (Matrosova et al. 2009; Volodin 2005). In matrilineal groups of yellow ground squirrels keys to individuality within a single recording session prevailed strongly over the keys to kinship (Matrosova et al. 2008); thus kin recognition in the matrilineal groups of this species can be based on the strong keys to individuality, kept at least within short terms. Such high short-term individuality also could provide yellow ground squirrels with information on the urgency of responding to the presence of a predator. Calls from multiple callers should evoke a more urgent response than calls from a single caller. Such a mechanism appears to function in yellow-bellied marmots and in Richardson's and speckled ground squirrels (Blumstein et al. 2004; Matrosova et al. 2009; Sloan and Hare 2006, 2008) and has been confirmed via computer modeling (Beauchamp and Ruxton 2007). Most likely, the highly individual-specific alarm calls allow the animals to estimate the number of callers producing alarms simultaneously.

After hibernation alarm calls retained their structure in the stable callers but underwent drastic changes in the unstable callers. Heterogeneity of individuals in the ability to keep the structure of alarm calls stable after hibernation also has been found in speckled ground squirrels (Matrosova et al. 2009). Similar to the current data on yellow ground squirrels, only one-third of the speckled ground squirrels retained stable alarm calls after hibernation. The consistency of these data is surprising because these 2 species are very different in size and biology. The speckled ground squirrel is small and lives under restricted visibility in dense grasses, with only acoustic and olfactory channels available for communication (Lobkov 1999; Tchabovsky 2005). The yellow ground squirrel is large and always rising above the vegetation, and is thus able to use visual channels for individual recognition as well (Popov 2007).

Given the low proportion of individuals with stable alarm calls, vocal identity within alarm calls cannot be the only modality sufficient to secure the recovery of personalized social relationships after hibernation in yellow ground squirrels. We hypothesize that individual recognition is likely to be based on a complex of behavioral traits and sensory modalities, including vocal identity encoded in the structure of the alarm calls, olfactory keys to identity (Mateo and Johnston 2000; Millesi et al. 2001), and appearance (Popov 2007). Such a multimodal encoding of identity should enhance the reliability of individual recognition and with it, the probability of restoring, after hibernation, social relationships from the previous year. At the same time, a multimodality of communicative signals ensuring individual recognition complicates thorough investigation of the keys to individual identity in ground squirrels.

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