Individual acoustic variation in Belding's ground squirrel alarm chirps in the High Sierra Nevada (L)

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The acoustic structure of calls within call types can vary as function of individual identity, sex, and social group membership and is important in kin and social group recognition. Belding's ground squirrels (*Spermophilus beldingi*) produce alarm chirps that function in predator avoidance but little is known about the acoustic variability of these alarm chirps. The purpose of this preliminary study was to analyze the acoustic structure of alarm chirps with respect to individual differences (e.g., signature information) from eight Belding's ground squirrels from four different lakes in the High Sierra Nevada. Results demonstrate that alarm chirps are individually distinctive, and that acoustic similarity among individuals may correspond to genetic similarity and thus dispersal patterns in this species. These data suggest, on a preliminary basis, that the acoustic structure of calls might be used as a bioacoustic tool for tracking individuals, dispersal, and other population dynamics in Belding's ground squirrels, and perhaps other vocal species.
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I. INTRODUCTION

Acoustic variation and distinctiveness is found in the vocal communication systems of all nonhuman animal species. The acoustic structure of calls within call types can vary as functions of individual identity, sex, and social group membership and is important in kin and social group recognition. Many species exhibit acoustic distinctiveness in various temporal and frequency parameters that likely provides the acoustic basis for individual or kin recognition (Chapman and Weary, 1990; Reby *et al.*, 1998a). In addition, dialects have been documented in many avian species (Adret, 1986; Sorjonen, 1987) and some cetacean species (pilot whales: Taruski, 1976, 1979; orcas: Ford and Fisher, 1983; Ford, 1991; bottlenose dolphins: McCowan *et al.*, 1998). Recent studies suggest that some primate species exhibit population and social group differences in call structure (chimpanzees: Mitani *et al.*, 1992; Mitani and Brandt, 1994; Marshall *et al.*, 1999; marmosets: Elowson and Snowdon, 1994) indicating a possible function for social recognition and/or cohesion. Several studies on avian species have reported dialectal differences in the song or calls of different populations, which are frequently consistent with differences in geographical location (Wright, 1996; Nelson, 1998).

Belding's ground squirrels (*Spermophilus beldingi*) are alpine-dwelling, social animals that live in colonies of related adult females and their dependent offspring (Armitage, 1981; Boellstorff and Owings, 1995). Sons appear to disperse from the natal burrow while daughters establish burrow systems adjacent to or overlapping that of their mother's. Adult males establish overlapping territories with those of the females before the breeding season and continue to defend these territories after the breeding season has ended.

Ground squirrels are vocal animals that respond to predators with alarm calls. These alarm calls have been variously named chatters, chats, whistles, squeals, chirps, and trills (Owings and Virginia, 1978; Owings and Leger, 1980; Leger *et al.*, 1984; Owings *et al.*, 1986). Whistles and chirps are harmonically structured narrow-band calls that have a relatively low fundamental frequency (given the body size of members of this species) between 2.8 and 5.1 kHz. Although the contexts and functions of ground squirrel alarm calls are relatively well known, the extent of acoustic variation in ground squirrel alarm vocalizations and whether such variation provides a basis for individual, kin, or group recognition remains mostly unexplored (Hare, 1999). The functions of chirps and whistles in predator and territory defense suggest that information on individual and social group identity might be present in these calls. Thus, the purpose of this study was to determine if the alarm chirps (whistles) of Belding's ground squirrels contained individual signature information that could provide the basis for individual and kin recognition. To address this goal, this preliminary study examined the alarm chirps of eight free-ranging adult female ground squirrels from four alpine lakes in the French Canyon of the High Central Sierra Nevada for individual differences and in relationship to the geographical locations of these ground squirrel populations.

II. METHODS

A. Subjects and study site

Subjects were eight free-ranging adult female ground squirrels. All subjects were identified as adults, determined by body size, and as females due to the proximity of dependent offspring. Subjects were recorded from four different alpine lakes in the French Canyon region of the High Sierra Nevada, approximately 12 miles west of Pine Creek Pack Station near Bishop, CA in the Owens valley. The lakes on which recordings of the eight different ground squirrels were conducted included Moon Lake ($n=3$), Elba Lake ($n=3$),

TABLE I. List of analyzed acoustic variables and their definitions.

Acoustic parameter	Description
Coefficient of frequency modulation McCowan and Reiss (1995) McCowan *et al.* (1998)	Calculated variable that represents the amount and magnitude of frequency modulation across a chirp, computed by summing the absolute values of the difference between sequential frequencies divided by 10 000.
Jitter factor Mitani and Brandt (1994)	Calculated variable that represents a weighted measure of the amount of frequency modulation, by calculating the sum of the absolute value of the difference between two sequential frequencies divided by the mean frequency. The sum result is then divided by the total number of points measured minus 1 and the final value is obtained by multiplying it by 100.
Frequency variability index Mitani and Brandt (1994)	Calculated variable that represents the magnitude of frequency modulation across a chirp, computed by dividing the variance in frequency by the square of the average frequency of a chirp and then multiplying the value by 10.
Minimum frequency	Lowest frequency attained by chirp, measured in Hz
Maximum frequency	Highest frequency attained by chirp, measured in Hz
Mean frequency	Calculated as a average frequency across chirp
Frequency range	Calculated as maximum frequency minus minimum frequency
Maximum frequency/Mean frequency	Calculated as maximum frequency divided by mean frequency
Mean frequency/Minimum frequency	Calculated as mean frequency divided by minimum frequency
Frequency at peak amplitude	Frequency at which the peak amplitude occurs in the chirp
Minimum frequency location	Location of minimum frequency in chirp, given as percentage of duration
Maximum frequency location	Location of maximum frequency in chirp, given as percentage of duration
Duration	Temporal distance of chirp, measured in ms
Location of peak amplitude	Location at which the peak amplitude occurs in the chirp, given as a % of duration
Start slope	Slope of the initial third of the chirp contour
Middle slope	Slope of the middle third of the chirp contour
Finish slope	Slope of the final third of the chirp contour

Alsace Lake ($n=1$), and L Lake ($n=1$). Each lake exhibited rocky montane terrain with intermittent evergreen trees, grass, and brush. Mountain passes, ranging from 0.7 to 1.8 km in distance and 152–305 m in altitude (which ranged from 3048 to 3505 m), separated each of the lakes.

B. Vocal recordings

One to three adult female ground squirrels from each of the four lakes were acoustically recorded on one of four days using an Audio-Technica AT4071 directional microphone (frequency response to 20 kHz) and a Sony D-10 Pro DAT Recorder (frequency response to 24 kHz). For this preliminary study, each lake was visited only once and recordings were conducted from 1 to 3 h at each site. To ensure that we recorded different individuals at each of the lakes, recordings were conducted near the burrow systems of individuals located at distinct locations around each lake. Each vocalization was individually identified by observing the animals vocalizing during call production (recordings were conducted within 6 m of each subject). The context of alarm calling for each individual was to presence of human observers as Belding's ground squirrels from this remote region are not habituated to humans. A total of 358 vocalizations were collected from the eight adult female ground squirrels at four alpine lakes during the study period (Moon: 93, 105, 14 vocalizations from three individuals, respectively, Elba: 67, 43, 5 vocalizations from three individuals, respectively, Alsace: 12 vocalizations from one individual, L Lake: 19 vocalizations from one individual). With the exception of one individual (Elba 3), multiple calling bouts ($n>2$), which were defined by an intersignal duration of at least 1 min, were recorded from each individual subject.

C. Acoustic analyses

All vocal recordings were digitized onto a Micron Pentium Computer using a Sound-Blaster soundcard (sampling rate up to 44.1 kHz) and Cool Edit Pro Signal Analysis software (sampling rate of 44.1 kHz and using 1024-point FFT with a Hamming filter). Acoustic files were filtered for background noise using standard parametric filtering in Cool Edit Pro on the Micron computer and cued for subsequent digital analysis.

The chirps recorded from each individual were measured using a modified version of the Contour Similarity Technique (for detailed descriptions of this technique, see McCowan, 1995; McCowan and Reiss, 2001). After call digitization and measurement were completed, several subsequent calculations were conducted. Several summary acoustic variables defining various call spectral, temporal, amplitude, and contour parameters (e.g., minimum frequency, maximum frequency, mean frequency, frequency range, duration, frequency, and location of the peak amplitude) were calculated from these measurements (see Table I for a list of analyzed parameters).

D. Statistics

The outcomes and covariates of the statistical tests were continuous in structure. Thus, discriminant function analysis and fixed effects linear regression were the statistical methods of choice (Pinheiro and Bates, 2000). Continuous variables were tested for normality. Because most variables required transformation, principal component analysis was conducted on the raw variables. All final statistical tests were conducted on the principal component values, which were

TABLE II. Percent correct classification from the discriminant analysis on the alarm chirps of individual Belding ground squirrels[a] from four high Sierra lakes.

		No. of cases classified into group								Comparison to random assignment (as "expected")		
Individual	% correct	Alsace1	Elba1	Elba2	Elba3	Moon1	Moon2	Moon3	L1	Total N	Fisher's exact	p
Alsace1	83	10	0	0	1	0	0	1	0	12	13.9	<0.0001
Elba1	54	0	25	7	1	12	1	1	0	47	33.8	<0.0001
Elba2	51	5	7	32	3	5	8	3	0	63	32.9	<0.0001
Elba3	80	0	0	1	4	0	0	0	0	5	19.2	<0.0001
Moon1	45	0	15	9	1	42	25	1	0	93	57.2	<0.0001
Moon2	64	0	12	18	0	8	67	0	0	105	90.8	<0.0001
Moon3	79	0	1	0	1	1	0	11	0	14	14.7	<0.0001
L1	100	0	0	0	0	0	0	0	19	19	25.9	<0.0001
										358		

[a]All factors in the order F1, F2, F3, F4 were entered into the discriminant function.

tested for and confirmed normality. Covariates included individual, calling bout, and "time of day" of the recording. "Time of day" and "calling bout" were insignificant for all analyses and thus removed from the models. All statistical tests were conducted using programmable S-Plus statistical software on a Pentium or Pentium II PC.

III. RESULTS

A. Principal components of ground squirrel chirp vocalizations

Principal component analysis on the chirp calls of the eight adult female Belding's ground squirrels generated 16 statistically independent components. Eigenvalues of the first four components met Kaiser's criterion of 1.00. These four components accounted for 82% of the variation in the original data set. Factor 1 represents measures of spectral shape (e.g., coefficient of frequency modulation, maximum frequency location, and minimum frequency location) and amplitudinal emphasis (e.g., the frequency and location of peak amplitude), as well as mean frequency and minimum frequency of chirps. Factor 2 represents another measure of spectral shape including the frequency range, jitter factor, maximum frequency/mean frequency, and the start slope of chirps. Factor 3 represents the duration and the frequency variability index. Factor 4 represents the middle and final slopes as well as the mean frequency/minimum frequency of chirps.

B. Individual differences in ground squirrel chirps

Belding's ground squirrels showed individual distinctiveness in the acoustic structure of their alarm chirps. Cross-validation discriminant analysis revealed that each individual could be reliably distinguished based upon the acoustic structure of their calls (see Table II, Fig. 1). The variables

(a)

	Alsace1	Elba1	Elba2	Elba3	Moon1	Moon2	Moon3	L1
Alsace1	0.0	27.4	13.2	15.0	24.7	18.3	22.0	113.5
Elba1		0.0	3.2	21.8	0.4	2.0	14.9	62.0
Elba2			0.0	13.4	2.4	1.3	12.4	73.4
Elba 3				0.0	17.6	18.0	4.9	51.4
Moon1					0.0	1.1	13.3	57.0
Moon2						0.0	16.8	68.9
Moon3							0.0	47.8
L1								0.0

(b)

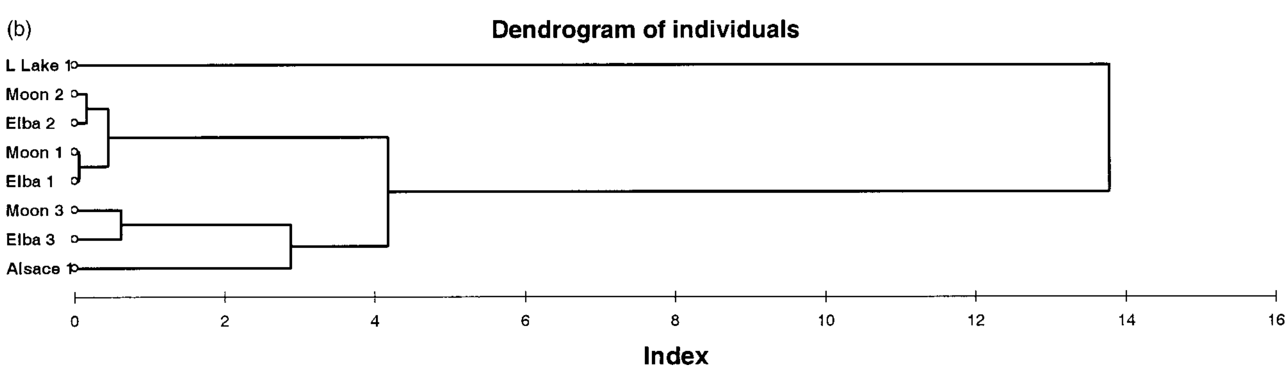

FIG. 1. (a) Mahalanobis distance generated from the discriminant function analysis between the alarm chirps of individual Belding's ground squirrels. (b) Dendrogram of Mahalanobis distance between the alarm chirps of individuals.

that contributed most to individual distinctiveness were factors 1 and 2, although all factors were entered into the discriminant function. Fixed effects linear regression confirmed the discriminant function analyses. Factor 2 significantly differed ($F_{7,350}=42.5$, $p<0.0001$) for each pairwise comparison at the 0.05 level using the Bonferroni method except Alsace1-Elba3, Alsace1-L1, Elba3-L1, Elba2-Moon2, Moon1-Moon2. Factor 1 significantly differed ($F_{7,350}=91.3$, $p<0.0001$) for three of the insignificant comparisons above: Alsace1-Elba3, Alsace1-L1, Elba3-L1 and factor 4 significantly differed ($F_{7,350}=30.2$, $p<0.0001$) for the remaining two insignificant comparisons: Elba2-Moon2, Moon1-Moon2.

In addition, a dendrogram generated from Mahalanobis distances from the discriminant analysis of individuals' alarm calls revealed that individuals from Elba Lake were more similar acoustically to individuals at Moon Lake than to each other, suggesting that acoustic similarity may represent a measure of genetic relatedness in this species (Fig. 1).

IV. DISCUSSION

Our preliminary results suggest that the alarm chirp vocalizations of adult female Belding's ground squirrels contain individual signature information which likely provides the basis for individual and kin recognition, as found in the vocalizations of several avian and mammalian species (Chapman and Weary, 1990; Reby *et al.*, 1998a). It is more likely that the acoustic differences found in this study are a result of genetic and not social influences, although the mechanisms underlying this acoustic variation will need to be evaluated in subsequent studies. Despite the mechanism(s), however, it might be possible to use this acoustic variation to track individuals and thus population dispersal patterns in this species using a noninvasive bioacoustic technique. Application of quantitative bioacoustic techniques might reveal subtle and important features of acoustic variation and patterns in free-ranging populations of many mammalian species (Reby *et al.*, 1998b). Therefore, we might effectively use bioacoustics as a tool for tracking population dispersal and dynamics, and possibly as a measure of genetic diversity, in other more threatened and endangered mammalian species, and thus in wildlife management and conservation.

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Armitage, K. B. (**1981**). ''Sociality as a life-history tactic of ground squirrels,'' Oecologia **48**, 36–49.

Adret-Hausberger, M. (**1986**). ''Temporal dynamics of dialects in the whistled songs of starlings,'' Ethology **71**, 140-152.

Boellstorff, D. E., and Owings, D. H. (**1995**). ''Home range, population structure, and spatial organization of California ground squirrels,'' J. Mammal. **76**, 551–561.

Chapman, C. A., and Weary, D. M. (**1990**). ''Variability in spider monkeys' vocalizations may provide basis for individual recognition,'' Am. J. Primatol **22**, 279–284.

Elowson, A. M., and Snowdon, C. T. (**1994**). ''Pgymy marmosets, *Cebulla pygmaea*, modify vocal structure in response to changed social environment,'' Animal Behaviour **47**, 1267–1277.

Ford, J. K. B. (**1991**). ''Vocal traditions among resident killer whales (*Orcinus orcinus*) in coastal waters of British Columbia,'' Ca. J. Zool. **69**, 1454–1483.

Ford, J. K. B., and Fisher, H. D. (**1983**). ''Group-specific dialects of killer whales (*Orcinus orca*) in British Columbia,'' in *Communication and Behavior of Whales*, edited by R. T. Payne (Westview Press, Colorado), pp. 129-161.

Hare, J. F. (**1999**). ''Juvenile Richardson's ground squirrels, *Spermophilus richardsonil*, discriminate among individual alarm callers,'' Anim. Behav. **55**, 451–460.

Leger, D. W., Berney-Key, S. D., and Sherman, P. W. (**1984**). ''Vocalizations of Belding's ground squirrels *Spermophilus beldingi*,'' Anim. Behav. **32**, 753–764.

Marshall, A. J., Wrangham, R. W., and Arcadi, A. C. (**1999**). ''Does llearning affect the structure of vocalizations in chimpanzees?'' Animal Behaviour **58**, 825–830.

McCowan, B. (**1995**). ''A new quantitative technique for categorizing whistles using simulated signals and whistles from captive bottlenose dolphins, *Delphindae Tursiops trucatus*,'' Ethology **100**, 177–193.

McCowan, B., and Reiss, D. (**2001**). ''The fallacy of 'signature whistles' in bottlenose dolphins: a comparative perspective of 'signature information' in animal vocalisations,'' Animal Behaviour **62**, 1151–1162.

McCowan, B., Reiss, D., and Gubbins, C. M. (**1998**). ''Social familiarity influences whistle acoustic structure in adult female bottlenose dolphins (*Tursiops truncatus*),'' Aquat. Mammals **24**, 21–40.

Mitani, J. C., and Brandt, K. (**1994**). ''Acoustic variability in the long distance calls of male chimpanzees,'' Ethology **96**, 233–252.

Mitani, J. C., Hasegawa, T., Gros-Louis, J., Marler, P., and Byrne, R. (**1992**). ''Dialects in chimpanzees?'' Am. J. Primatol. **27**, 233–243.

Nelson, D. A. (**1998**). ''Geographic variation in song of Gambel's white-crowned sparrow,'' Behaviour **135**, 321–342.

Owings, D. H., and Leger, D. W. (**1980**). ''Chatter vocalizations of California ground squirrels: predator and social-role specificity,'' Z. Tierpsychol. **54**, 163–184.

Owings, D. H., and Virginia, R. A. (**1978**). ''Alarm calls of California ground squirrels *Spermophilus beecheyi*,'' Z. Tierpsychol **46**, 58–70.

Owings, D. H., Hennessy, D. F., Leger. D. W., and Gladney, A. B. (**1986**). ''Different functions of ''alarm'' calling for different time scales: a preliminary report,'' Behaviour **99**, 101–116.

Pinheiro, J. C., and Bates, D. M. (**2000**). *Mixed-Effects Models in S and S-Plus* (Springer, New York).

Reby, D., Joachim, J., Lauga, J., Lek, S., and Aulagnier, S. (**1998a**). ''Individuality in the groans of fallow deer (*Dama dama) bucks*,'' J. Zool. **245**, 79–84.

Reby, D., Hewison, A. J. M., Cargnelutti, B., Angibault, J. M., and Vincent, J. P. (**1998b**). ''Use of vocalizations to estimate population size of roe deer,'' J. Wildlife Management **62**, 1341–1347.

Sorjonen, J., (**1987**). ''Temporal and spatial differences in the traditions and repertoires in the song of a thrush nightingale (Luscinia luscinia),'' Behaviour **102**, 196–212.

Tarurski, A. G., (**1976**). ''Whistle of the pilot whale Globicephala spp.: variations in whistling related to behavioral-environmental context, broadcast of underwater sounds, and geographic locatioin.'' Ph.D. dissertation, University of Rhode Island, Kingston.

Taruski, A. G. (**1979**). ''The whistle repertoire of the North Altantic pilot whale (Globicephala melaena) and its relationship to behavior and environment,'' in Behavior of Marine Animals, edited by H. E. Win and B. L. Olla, Vol. 3: Cetaceabs (Plenum Press, New York), pp. 345—368.

Wright, T. F. (**1996**). ''Regional dialects in the contact call of a parrot,'' Proc. R. Soc. London, Ser. B **263**, 867–872.