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Report

Social Group Size Predicts the Evolution of Individuality

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Summary

Discriminating among individuals is a critical social behavior in humans and many other animals [1–3] and is often required for offspring and mate recognition, territorial or coalitional behaviors, signaler reliability assessment, and social hierarchies [4–9]. Being individually discriminated is more difficult in larger groups, and large group size may select for increased individuality–signature information–in social signals, to facilitate discrimination [4, 10–14]. Small-scale studies suggest that more social species have greater individuality in their social signals, such as contact calls [4, 12, 13]. However, this relationship has not been evaluated in a broader-scale evolutionary context or in social signals other than contact calls. It is not yet known whether social group size may be viewed as a general evolutionary driver of individuality. Here we show a strong positive evolutionary link between social group size in sciurid rodents and individuality in their social alarm calls. Social group size explained over 88% of the variation in vocal individuality in phylogenetic independent contrasts. Species living in larger groups, but not in more complex groups, had more signature information in their calls. Our results suggest that social group size may promote the evolution of individual signatures and that the sociality-individuality relationship may be a general phenomenon in nature.

Results

Discriminating among individuals is important for social animals [2, 3, 7, 8], and it often benefits individuals not only to discriminate among or between others but also to be discriminated by others [1, 2, 4–6, 8, 9]. Social animals experience selective pressure to clearly signal their individual identity to others, a task that becomes more difficult as the number of signalers increases [10, 11]. When discrimination at the individual level is important to a species' social behaviors, the amount of individualistic information in their signals must be sufficient to permit discrimination among the individuals that routinely interact socially using these signals. We therefore expect that individuality should evolve with the size of a species' typical social group (first proposed in [10], see also [4, 11–14]). Previous comparisons across pairs or small numbers of species have indicated a relationship between communal crèche size and individuality in parent-offspring contact calls [4, 12, 13], but a broader-scale evolutionary relationship between social group size and individuality has not yet been tested. Here we present the first phylogenetically controlled independent-contrasts study of the relationship between individuality and social group size, and the first to examine social signals other than contact calls.

To test the hypothesis, we calculated the amount of individuality contained in a social signal, vocal alarm calls, and compared this across eight species of sciurid rodents that vary in social group size and social structure complexity (Figure 1). Ground-dwelling sciurids have individualistic alarm calls, are recognized by group mates based on these calls, and stand to reap fitness benefits from being recognized ([5, 7, 8, 15, 16]; see also the Supplemental Information available online).

Individuality occurs when interindividual variation in a signal exceeds intraindividual variation in that signal. This individuality can be quantified using information theory [11]. We used Beecher's information statistic, H_s [4, 10, 11, 13, 14, 17], to quantify the vocal individuality present in the alarm calls and compared this with group size data taken from the literature. As predicted, individuality was positively related to social group size (R^2 = 0.888, y = 0.572x + 1.628, p < 0.001, n = 8; Figure 2A) in the raw data.

We used phylogenetic independent contrasts and regression to control for phylogeny and identify the correlated evolution between individuality and group size. As predicted, contrasts of social group size were significantly correlated with contrasts of individuality (R^2 = 0.887, y = 0.519x, p < 0.001, n = 7 independent contrasts; Figure 2B).

Among species living in stable social groups, we expected group size to be the major predictor of evolutionary changes in individuality. However, animal species differ not only in their group size but also in how their groups are structured, and we wanted to control for this. Social structure complexity may be quantified in a variety of ways [18–21] and may influence individuality. The social reproductive complexity of paper wasps influences facial individuality [22]. In sciurids, social complexity influences the size of vocal repertoires [18], but its influence on individuality, if any, is unknown. We therefore controlled for three measures of social structure complexity [18, 20, 21] in our study. Group size and social structure complexity were not intercorrelated in our data (see below) and are not necessarily correlated in nature [19].

We regressed individuality separately against social group size, Armitage's sociality index [20], Michener's social grade [21], and Blumstein and Armitage's social complexity index [18]. In the raw data, individuality was unrelated to social grade (R^2 = 0.148, y = −0.246x + 6.856, p = 0.347), sociality index (R^2 = 0.375, y = −0.473x + 7.536, p = 0.107), or social complexity index (R^2 = 0.177, y = −0.901x + 6.796, p = 0.300) (n = 8 in all cases). We performed multiple regressions with backward elimination to determine whether each index of social structure complexity interacted with social group size to influence individuality and/or explained additional variation. The social complexity indexes and any interactions containing them were not significant and were dropped from each model until only social group size remained.

We performed the same regressions on independent contrast data to control for effects of phylogeny. Individuality

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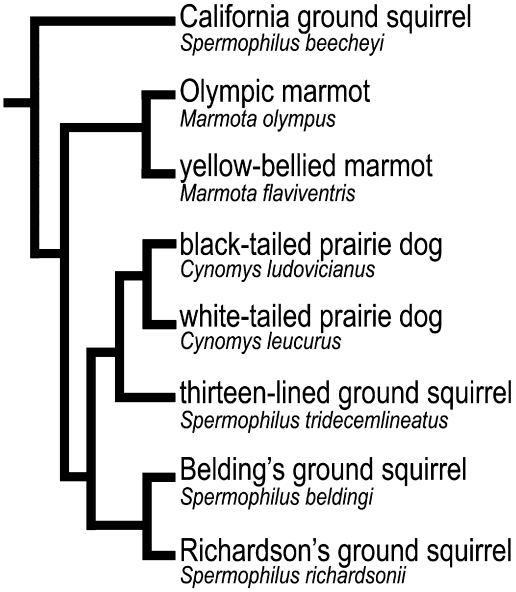


Figure 1. Phylogeny of Study Taxa

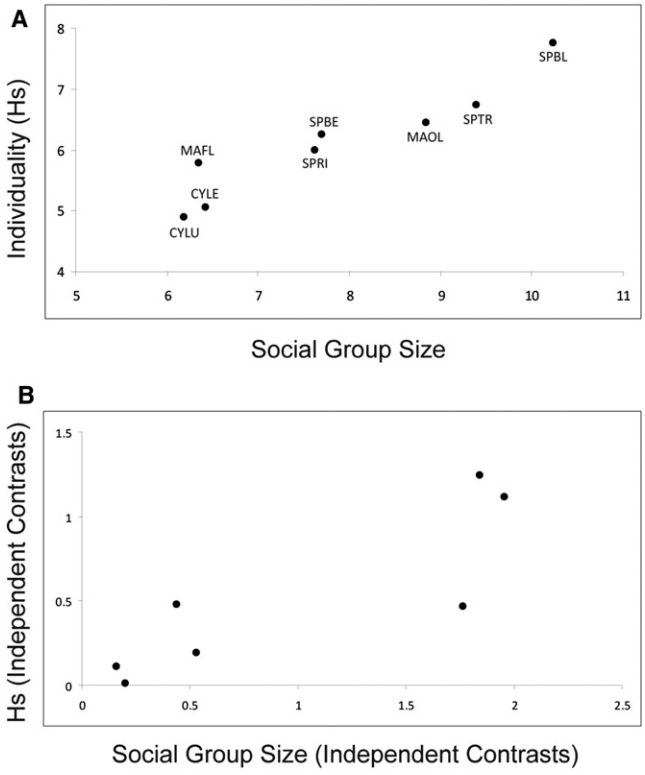


Figure 2. Social Group Size versus Vocal Individuality for Eight Species of Ground-Dwelling Sciurids

(A) Group size versus individuality (raw data; n = 8). Data points are labeled by species: *C. leucurus* (CYLE), *C. ludovicianus* (CYLU), *M. flaviventris* (MAFL), *M. olympus* (MAOL), *S. beecheyi* (SPBE), *S. beldingi* (SPBL), *S. richardsonii* (SPRI), *S. tridecemlineatus* (SPTR).

(B) Group size versus individuality (independent-contrasts data, positivized; n = 7).

was not evolutionarily correlated with any social complexity index (Armitage's sociality index [20]: R^2 = 0.224, y = −0.378x, p = 0.236; Michener's social grade [21]: R^2 = 0.095, y = −0.191x, p = 0.457; Blumstein and Armitage's social complexity index [18]: R^2 = 0.076, y = −0.669x, p = 0.509) (n = 7 independent contrasts in all cases). As with the raw data, indexes of social structure complexity dropped out of multiple regressions in which they were entered, leaving only social group size.

Discussion

Animals often benefit by discriminating individuals [2, 3, 7, 8] and by signaling their individual identity to others [2, 5, 8]. For example, territory holders, socially ranked individuals, parents, offspring, mates, coalition partners, and alarm signalers benefit by being recognized by their neighbors, group members, kin, mates, or companions [1, 4–6, 8, 9]. This recognition utilizes individualistic signatures (individuality) in animals' social signals. Being discriminated from other conspecifics is more difficult in larger groups because there are more distracters and targets to be sifted through. A greater degree of individuality is thus required for successful discrimination in larger groups [4, 10–14] and should evolve when individually discriminating animals increase their group size on an evolutionary timescale. Our results support this expectation. In both the raw data and independent contrasts, typical social group size explained over 88% ($p < 0.001$) of the variation in vocal individual distinctiveness across species. It thus seems likely that selection for individuality is stronger in species that must routinely interact with more individuals.

Individuality in Other Signals and Other Taxa

Our study's hypothesis [4, 10–14] predicts that the number of individuals that must be discriminated (group size) should positively affect the amount of individuality in signals used for discrimination, provided that signalers benefit from being discriminated. These conditions are met in a variety of signal contexts [1, 2, 4–6, 8, 9]. Individuality has been found in various social signals, and the degree of individuality has been found to relate to social group size in avian and chiropteran contact calls [4, 12, 13] and in rodent alarm calls (this study). We expect a positive evolutionary relationship between group size and individuality to be common in other social communicative signals, and in other taxa as well.

Our group size-individuality hypothesis is relevant to taxa in which social groups are relatively stable and individual discrimination among group members is important. Some animal species have a hierarchy of nested grouping levels (e.g., fission-fusion) or may exhibit different types of social interaction (e.g., solitary animals with contiguous range borders). Animals may use different social signals to communicate at these different levels. For a given social signal, the relevant level of group should provide the selective pressure for individuality in those signals. For instance, the size of a communicating "group" of solitary-living animals would likely predict the extent of individualistic information in their territorial marks. The degree of individuality in a given signal could furthermore provide clues to the social group level at which the signal is typically used. The relationship should hold even if only one or a few receivers must discriminate among multiple signalers: for instance, the number of client fish visiting the same cleaner station may predict the individuality in their bodily markings. Such relationships remain to be tested.

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Table 1. Location and Recording Data for Each Study Species

Species	Recorded by	Year	Site	Location	Approximate Coordinates
C. leucurus	K.A.P.	2006	Arapaho National Wildlife Refuge	Jackson County, CO	40° 37′ N, 106° 16′ W
C. ludovicianus	K.A.P.	2006	UL Bend National Wildlife Refuge	Phillips County, MT	47° 56′ N, 107° 52′ W
M. flaviventris	D.T.B.	2001, 2002, 2003	Rocky Mountain Biological Laboratory	Gunnison County, CO	38° 55′ N, 106° 60′ W
M. olympus	S.C. Griffin	2004, 2005	Olympic National Park	Clallam County, WA	47° 49′ N, 123° 13′ W
S. beecheyi	K.A.P.	2006, 2008	Sedgwick Reserve (University of California Natural Reserve System)	Santa Barbara County, CA	34° 42′ N, 120° 2′ W
S. beldingi	K.A.P.	2007	Rock Creek Canyon/Lower Horse Corral	Mono County, CA	37° 25′ N, 119° 0′ W
S. richardsonii	J.F. Hare	2006	Assiniboine Park Zoo property	Winnipeg, MB	49° 52′ N, 97° 14′ W
S. tridecemlineatus	K.A.P.	2005	Shortgrass Steppe Long-Term Ecological Research Station	Weld County, CO	40° 44′ N, 104° 44′ W

We do not expect the group size-individuality relationship to hold for all animal taxa. For animals in relatively fluid or impersonal aggregations (e.g., some ungulate herds, fish schools, or insect swarms), individual interaction is less important and group membership is unstable. In such cases, it may be less important to discriminate individuals. Eusocial species also may not benefit as much from discrimination at the individual level; group membership discrimination may be more critical. The relationship between group size and individuality is less likely to hold for such situations, but this remains to be tested.

Sociality as a Driver of Individuality

Signaling or attending to individual identity is important in a wide range of social communicative encounters in many taxa, and it hinges on the social importance of attending to underlying individual differences such as behavioral tendencies, past or continuing condition, or past actions (e.g., [2, 3]). Signalers should indicate their individual identity whenever they benefit by having their behavioral tendencies, personal history, etc. known by others [2]. Such a socioecological environment exists for a range of animal species, including humans and other primates, marine mammals, social rodents, social carnivores, equines, elephants, and many birds. We expect that the individuality-sociality relationship may be a widespread phenomenon in nature.

Larger social groups require more intricate individual signatures for effective discrimination, and our results implicate sociality as a major predictor of individuality. The bigger the crowd, the more it takes to stand out.

Experimental Procedures

Data Collection

Eight species of ground-dwelling sciurid rodents were selected to represent a range of group sizes and social complexity levels, as well as phylogenetic diversity (Figure 1; Table 1). All eight species live in social groups and produce vocal alarm calls in response to predatory stimuli. Refer to Supplemental Information for details on why individuality is important in alarm signals. Animal procedures conformed to all regulatory standards and were approved by the animal care and use committees of the University of California, Los Angeles; University of California, Santa Barbara; University of Montana; and University of Manitoba. We captured animals using live traps baited with peanut butter, horse feed, and/or fruit. If the animal vocalized in the trap when the researcher approached, these calls were recorded. The animals were then weighed, sexed, and individually marked with numbered ear tags and/or hair dye, then released at the capture site. Alarm calls were elicited by human presence (see [14]). The researcher walked toward the focal animal and recorded calls that the animal produced in response to being approached. When possible, we recorded calls from individuals within traps because this ensured high recording quality. Some species do not normally alarm call in live traps; these species were given individualistic dye markings, released, and later approached on foot to elicit and record calls (Supplemental Information).

Compared to other aspects of sociality (e.g., [19, 21, 23, 24]), we expected social group size to have the largest effect on the need for individuality in social signals such as alarm vocalizations (see also [11]). The number of individuals that live together, and hence the number of individuals that must be routinely discriminated, is the major factor affecting the difficulty of discrimination tasks and the amount of individualistic information that an animal must produce to be discriminated [4, 11, 14]. Individuals within the social group are those most often in close proximity and those heard most often, and are presumed to be intended recipients of signals (such as alarm calls) given by group members. Species-typical social group size (Table 2) was calculated from demographic data (Supplemental Information). Social groups are defined by mutual cooperation and/or amicability (burrow sharing, alarm calling, assistance during chases, and/or cooperative defense of territories and young). Boundaries between such social groups are easily identified by increased agonism, territoriality, and/or lack of influence on alarm calling rates. Social groups are labeled by different terms in different taxa (Table 2; Supplemental Information).

Acoustic Processing and Measurements

We measured 20 high-quality calls each from ten individuals per species, for a total of 1600 calls. To control for potential bout-specific call traits, we used calls from at least two distinct calling bouts per individual, with no single bout contributing more than ten calls. We considered bouts distinct if they were separated by at least 20 minutes of noncalling during which the animal resumed normal, nonvigilant behavior (e.g., feeding, grooming). Bouts were typically separated by a few days.

Table 2. Individuality, Group Size, and Social Complexity Indices for Eight Sciurid Species

Species	Sociality Index [20]	Social Grade [21]	Social Complexity [18]	H_s	Group Size	Type of Group	Group Size Sources
C. leucurus	3	2	0.84	5.05	6.42	clan	[30–32]
C. ludovicianus	5	5	1.12	4.89	6.19	coterie	[30, 33]
M. flaviventris	4	4	1.06	5.79	6.35	matriline	[19, 34–36]; Supplemental Information
M. olympus	4	5	1.46	6.45	8.84	colony	[37]
S. beecheyi	2	2.5	0.26	6.26	7.70	family	[38–40]
S. beldingi	2	2	0.40	7.76	10.23	kin group	[41]; Supplemental Information
S. richardsonii	2	2	0.39	6.00	7.63	family	[42, 43]
S. tridecemlineatus	2	1.5	0.50	6.74	9.39	family	[44–47]

H_s is Beecher's information statistic.

We either recorded directly to digital files or digitized call recordings to 16-bit 48 or 44.1 kHz .aif files, then normalized each call to 95% maximum amplitude. Using consistent settings, we made a series of measurements in the time, frequency, and relative amplitude domains (Supplemental Information).

Data Analysis

We standardized the acoustic data according to Beecher [11] before calculating principal components (Supplemental Information). We calculated Beecher's information statistic (H_s, [10, 11]) for each species from the principal components, using all F values that were significant at the $\alpha = 0.05$ level. Beecher's statistic is a standard measure used to quantify individuality [4, 13, 14, 17]. It expresses a signal's ability to reduce a receiver's initial uncertainty about the identity of the signaler down to a minimum level (the within-individual error) and can quantify individuality across disparate characteristics and modalities. With consistent sampling, the information statistic can be directly compared across species or signal types [4, 17]. The more bits of individualistic information in a signal, the easier it is to discriminate individuals, and the more total individuals can be reliably discriminated [10, 11].

We calculated independent contrasts (Supplemental Information) using phylogenetic tree hypotheses from Harrison et al. [25] and Herron et al. [26]. We chose Felsenstein's method [27] because it is a standard phylogenetic tool used in evolutionary studies of morphological, behavioral, and social traits, including group size (see [28, 29]).

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures and can be found with this article online at doi:10.1016/j.cub.2011.01.051.

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Current Biology, Volume *21*

Supplemental Information

Social Group Size

Predicts the Evolution of Individuality

Kimberly A. Pollard and Daniel T. Blumstein

Supplemental Experimental Procedures

Individuality in Alarm Calls

For individuality to be selectively favored in a signal context, animals must benefit from being individually discriminated in that signal context. In many signal contexts, the value of being individually discriminated is straightforward. For example, we expect strong evolutionary pressure for parent-offspring contact calls to be individualistic (i.e., an unrecognized offspring may not get fed by its parent). For contact calls, it is clearly in the signaller's genetic interest to be individually discriminated.

The value of individual discrimination in an alarm context is more complex, but nonetheless highly important in the daily lives of many social animals. In many species, it is in the caller's genetic interest to be individually discriminated via their alarm calls. Individually-recognized callers have been shown to benefit from focused acts of reciprocation [9] and may also gain status or mating benefits from their alarm efforts (as suggested in [48]). Alarm-calling is also a form of nepotism in many species [49-56], and individual signatures in these calls can further enhance the nepotistic value of alarm calls [5, 8, 16]. Individual signatures allow a caller's kin to fine-tune their antipredator response, incorporating information about the individual caller's unique alarm thresholds and reliability [7, 8, 15, 16, 57-60].

This nepotistic benefit of individualistic alarm calls may be particularly important for sciurid rodents. These animals live in groups of closely-related kin and alarm call nepotistically [49, 50, 53, 54, 56]. Sciurid alarm calls are individualistic [14, 17, 61], and social group-mates discriminate individuals based on their alarm calls [5, 62, see also 63]. Listeners furthermore adjust their antipredator response based on the recognized caller's alarm history [7, 8, see also 15, 60], and they benefit from doing so [8, 16, 64, see also 15, 60]. By encoding individualistic signatures in their alarm calls, callers assist their kin with this individual discrimination task [5, 8, 16]. Individually-recognized alarm callers thus stand to benefit via kin selection and may also reap direct benefits via reciprocation or status enhancement.

Special Note on Field Methods

Most ground-dwelling sciurids do not encode predator-specific information in their alarm calls [65-68], but prairie dogs may do so [69, 70]. To control for this, a single researcher (KAP) conducted all approaches on prairie dogs and wore identical clothing during each approach.

Group Size Calculations

For independent-family-living species, group sizes were defined as the litter size plus one (to include the mother). Litter, harem, coterie, and clan sizes were taken from primary sources in the published literature (Table 2), weighted by sample size, and averaged. The typical matriline size for yellow-bellied marmots was calculated from litter size, reproductive rates, recruitment rates, and sex ratio data (A). The typical kin group size for Belding's ground squirrels was calculated from litter size, reproductive rates, and survivorship data (B and C).

(A) Calculation of Matriline Size in Yellow-Bellied Marmots

Value	Variable	Source
1.47	mean adult females in a matriline	Armitage 1991 (34)
0.5769	proportion YF that are retained	Blumstein et al. 2009 (35)
0.3087	proportion YM that are retained	Blumstein et al. 2009 (35)
0.3404	AM per AF in a matriline	Olson 2009 (36)
4.3	mean litter size	Blumstein & Armitage 1998 (19)
0.48	proportion adult females breeding	Blumstein & Armitage 1998 (19)

Total Matriline

AF	AM	juveniles	retained YF	retained YM	total typical matriline size
1.47	0.5004	3.0341	0.8752	0.4683	6.3481

Typical numbers of members of each age-sex class (adult females (AF), adult males (AM), yearling females (YF), yearling males (YM), and juveniles) were calculated from demographic data and summed to estimate the typical matriline size for yellow-bellied marmots.

For example, the number of juveniles in a typical matriline was calculated as the average number of adult females in a matriline * the proportion of these females that are breeding * the mean litter size = (1.47)*(0.48)*(4.3) = 3.03.

(B) Demographic Data for Belding's Ground Squirrels

Age in years n	Age-specific fecundity (litter size) Fn	Estimated survivorship (1-qx) Sn
0	0.0000	0.3858
1	2.0800	0.5040
2	4.3424	0.5276
3	4.8960	0.5224
4	6.2263	0.5429
5	3.7500	0.4737
6	3.1500	0.5556
7	4.0000	0.8000
8	2.8800	0.2500
8+	3.2640	0.0000

Age-specific fecundity (F_n) and survivorship (S_n) used to calculate kin group size for Belding's ground squirrels. All data in this table were taken from Sherman and Morton 1984 (ref. 41).

(C) Calculation of Kin Group Size in Belding's Ground Squirrels

Year A

	mom (2F)	focal (JF)	littermate sisters (JF)	littermate brothers (JM)	non-littermate sisters (YF)
	1	1	1.1712	2.1712	0.4012
their yy		0	0	0	0.8345

total group size = 6.5781

Year B

	mom (3F)	focal (YF)	littermate sisters (YF)	littermate brothers (YM)	non-littermate sisters (2F)
	0.5276	1	0.4518	(dispersed)	0.2022
their yy	2.5829	2.0800	0.9397	N/A	0.8780

total group size = 8.6622

Year C

	mom (4F)	focal (2F)	littermate sisters (2F)	non-littermate sisters (3F)	daughters (YF)	non-littermate sisters (YF)
	0.2756	1	0.2277	0.1067	0.4012	0.4982
their yy	1.7159	4.3424	0.9887	0.5222	0.8345	1.0362

total group size = 11.9493

Year D

	mom (5F)	focal (3F)	littermate sisters (3F)	non-littermate sisters (4F)	daughters (2F)	non-littermate sisters (2F)	daughters (YF)	non-littermate sisters (YF)
	0.1496	1	0.1201	0.0557	0.2022	0.2511	0.8376	0.3310
their yy	0.5610	4.8960	0.5881	0.3469	0.8780	1.0903	1.7421	0.6884

total group size = 13.7380

Mean group size over 4 years of life = 10.2319

Belding's ground squirrels exhibit active and cohesive cooperation among close female kin, a different social grouping than that seen in other ground squirrels [71, 72]. To estimate the typical kin group size for Belding's ground squirrels, we consider a focal female with a typical lifespan given survival to adulthood [41]. We then calculate the average kin group size that focal individual experiences across those years. The typical kin group for a given year encompasses the average number of surviving, non-dispersed close kin (the focal animal plus her adult daughters, mother, adult sisters, and the current young of the year from these classes [71, 72]). Behavior among close kin in Belding's ground squirrels is defined by amicability, cooperative behavior, protective behavior, and effect on alarm calling. Behavior toward individuals outside the close kin group is characterized by hostility [71, 72]. J = juvenile, Y = yearling, 2F = two year old adult female (etc.), yy = young of the year.

Values in this table were calculated from fecundity and survivorship data shown in (B). For example, the number of littermate sisters living in year D is calculated as follows:

$$\text{littermatesisters}_D = (F_2/2 - 1)(S_0)(S_1)(S_2) = (4.3424/2 - 1)(0.3858)(0.5040)(0.5276) = 0.1201$$

F_2 indicates the original litter size (born from a mother that at the time was two years old). This is divided by 2 to include only the female pups (equal sex ratio is assumed). 1 is subtracted from this number because one of the female pups is the focal individual. The remaining female pups are the focal's littermate sisters. S_n is the probability an individual survives year n of their life (given that they are alive at the start of year n). The littermate sisters living in year D are only those that survived years A, B, and C.

Acoustic Settings and Computer Programs

We measured acoustic traits using Canary 1.2.4 [73], with consistent settings (spectrogram: fast Fourier transformation, FFT, size = 1024 points, overlap = 99.61%, frame length = 256 points, clipping level = -80 dB, window function = Blackman, amplitude = logarithmic, display style = boxy; spectrum: FFT size = 512 points, overlap = 99.8%, frame length = 512 points, clipping level = -80 dB, window function = Blackman, amplitude = logarithmic). For most species, measurements were made in the region between peak amplitude and 40 dB below peak amplitude. It was necessary to utilize a different range to achieve the best screen resolution for white-tailed prairie dogs (to 20 dB below peak) and black-tailed prairie dogs (to 30 dB below peak).

We used SPSS 13.0 [74] to calculate principal components from the acoustic dataset (minimum eigenvalue = 0.01, 25 iterations, correlation method), and these were then used to calculate Beecher's information statistic for individuality [10, 11].

To control for phylogeny, we entered individuality, group size, and social structure complexity data for each species into Mesquite 1.04 [75] and used the PDAP module [76] to calculate independent contrasts. The resulting contrasts were entered into a general linear model using SPSS 13.0 [74].

Names and Descriptions of Signal Traits Measured from Alarm Calls

Measurement	*Description*	*Species*[†]						
		Richardson's	*Olympic*	*California*	*white-tailed*	*black-tailed*	*Belding's*	*thirteen-lined*
peak frequency	The dominant frequency (frequency where the most energy is focused), as measured from the spectrogram of the main call.	X	X	X	X	X	X	X
low frequency	The lowest frequency of any band at any point in the main call, measured from the spectrogram.	X	X	X	X	X	X	X
high frequency	The highest frequency of any band at any point in the main call, measured from the spectrogram.	X	X	X	X	X	X	X
total bandwidth	The total bandwidth of the main call (change in frequency from the highest point to the lowest point, measured from the spectrogram).	X	X	X	X	X	X	X
time until major inflection point (MIP)	The time from the beginning of the call to the major inflection point (MIP), measured from the spectrogram. We define the MIP as the point in the call when the slope of the F1 band changes most abruptly.	X						
major inflection point type	Four types of MIPs were observed in Richardson's calls. A qualitative measure, later numerically coded, was taken from the spectrogram to define the MIP type for a particular call (angle, curve, split, or gap).	X						
MIP angle	The angle made by the upper edge of the F1 band at its major inflection point, measured from the spectrogram.	X						
call shape	A qualitative measure, later numerically coded, describing the shape of the main call in the spectrogram. E.g., whether the band shape looks most like a slant, arc, sine curve, dip, flat line, etc. For Richardson's, the call shape was recorded for the back half of the call (the content of the call after the major inflection point).	X	X	X	X	X	X	X

# harmonics	The number of harmonics (bands above the fundamental frequency at integer multiples of the fundamental frequency) visible in the spectrogram. For Richardson's we counted the number of harmonics in the front half of the call (before the MIP) and in the back half of the call (after the MIP) as separate measures.	X	X	X	X	X	X	X
# continuous harmonics	The number of harmonics visible in the spectrogram that cover at least 80% of the duration of the call. For Richardson's, the number of continuous harmonics in the front half of the call (before the MIP) and in the back half of the call (after the MIP) were separate measures.	X	X	X		X		
emphasized harmonic	The loudest harmonic in the call, i.e., the darkest harmonic in the spectrogram throughout the call's length. For Richardson's the emphasized harmonic was measured in the front half and the back half of the call as separate measures.	X	X	X	X	X	X	X
# subharmonics	The maximum number of subharmonic bands appearing between any two main bands in the call.			X		X	X	
subharmonic bursts	Indicates which trill bursts contain subharmonics.						X	
sideband presence	Indicates whether there are sidebands in a call. We define sidebands as short bursts occurring above and/or below main bands but not evenly spaced between bands (distinct from subharmonics).						X	
sideband bursts	Indicates which trill bursts contain sidebands.						X	
sideband location	Indicates whether sidebands are predominantly above, below, or above and below most bands where they occur.						X	
entire F0* bandwidth	The bandwidth (frequency range) covered by the fundamental frequency band (F0) during its entire duration, measured from the spectrogram	X	X	X	X	X	X	X

F0 bandwidth (front)	The bandwidth (frequency range) covered by the fundamental frequency band (F0) during its entire duration between the start of the call and the MIP, measured from the spectrogram	X						
F0 bandwidth (back)	The bandwidth (frequency range) covered by the fundamental frequency band (F0) during its entire duration between the MIP and the end of the call, measured from the spectrogram	X						
F0* starting low	The lowest frequency covered by the fundamental frequency band (F0) at the very beginning of the main call, measured from the spectrogram.	X	X	X	X	X	X	X
F0* starting high	The highest frequency covered by the F0 band at the very beginning of the main call, measured from the spectrogram	X	X	X	X	X	X	X
F0* ending low	The lowest frequency covered by the fundamental frequency band (F0) at the very end of the main call, measured from the spectrogram	X	X	X	X	X	X	X
F0* ending high	The highest frequency covered by the F0 band at the very end of the main call, measured from the spectrogram	X	X	X	X	X	X	X
typical F0* bandwidth	The thickness (bandwidth) of the F0 band, measured from a slice in the spectrogram where the call is the most flat. For species with trills, this was measured from the middle burst.	X	X	X	X	X	X	X
call duration	The time passed between the beginning and end of the call, measured from the waveform or spectrogram.	X	X	X	X	X	X	X
time until maximum amplitude	The time passed between the beginning of the call and the instant where the maximum amplitude is reached, measured from the waveform. The maximum amplitude occurs where the waveform is the thickest.	X	X	X	X	X	X	X

chuck duration	The time passed from the beginning to the end of the chuck, measured from the waveform. We define a chuck as a separate short set of bands, usually sharply decreasing in frequency at the end of a Richardson's call.	X						
chirp duration	The time passed from the beginning to the end of the chirp, measured from the spectrogram. We define a chirp as the first major note in a California ground squirrel call (excluding warbles, etc.) The chirp portion is largely tonal and has harmonic structure.			X				
maxamp in chirp	Whether or not the instant of maximum amplitude occurs within the chirp of a California ground squirrel call.			X				
click/chuck before	Indicates whether the call contains any clicks or chucks and whether these are before the main call. We define a click as a fairly solid vertical line of sound in the spectrogram and a chuck as a small piece of sound with harmonic structure shortly before or after a black-tailed prairie dog call.					X		
click/chuck after	Indicates whether the call contains any clicks or chucks and whether these are after the main call.					X		
band doubling front	Indicates whether band-doubling occurs in the front third of the call. Band doubling occurs when a major frequency band appears as two tightly-stacked bands, yielding forked frequency peaks in a spectrum.					X		
band doubling middle	Indicates whether band-doubling occurs in the middle third of the call.					X		
band doubling back	Indicates whether band-doubling occurs in the back third of the call.					X		

F0 frequency	The frequency of F0, measured from a spectrum slice of the call. For Richardson's, the slice was taken at the center of the back half of the call. For all others, the slice was taken at the instant of the call's maximum amplitude.	X	X	X	X	X	X	X
F1…Fn frequency	The frequencies of F1 through Fn, measured from a spectrum slice of the call. For Richardson's, the slice was taken at the center of the back half of the call. For all others, the slice was taken at the instant of the call's maximum amplitude.	X	X	X		X	X	X
order of band emphasis	The order of bands in terms of loudness (darkness throughout their length on the spectrogram).	X	X	X		X	X	X
dB F0	The amplitude of F0, measured from a spectrum slice of the call. For Richardson's, the slice was taken at the center of the back half of the call. For all others, the slice was taken at the instant of the call's maximum amplitude.	X	X	X	X	X	X	X
dB F1…Fn	The amplitudes of F1 through Fn, measured from a spectrum slice of the call. For Richardson's, the slice was taken at the center of the back half of the call. For all others, the slice was taken at the instant of the call's maximum amplitude.	X	X	X	X	X	X	X
# harmonics in intro sequence (IS)	The number of harmonics visible in the spectrogram of the intro sequence (IS). We define an IS as a short burst of scrunched bands at the beginning of an Olympic marmot call.		X					
F0 at center of IS	The frequency of the F0 in the IS, measured from a spectrum slice of the call. The slice was taken at the center of the IS.		X					
F1…Fn at center of IS	The frequencies of the F1 through Fn in the IS, measured from a spectrum slice of the call. The slice was taken at the center of the IS.		X					

order of band emphasis in IS	The order of bands in the IS in terms of loudness (darkness throughout their length on the spectrogram).		X					
IS duration	The time passed between the beginning and end of the IS, measured from the waveform.		X					
# grumbles	The number of grumbles visible in the spectrogram. We define grumbles as small stacks of brief, low-pitched bands that appear after a California ground squirrel chirp.			X				
uniformity of grumble gaps	Qualitative assessment, later numerically coded, of whether or not the grumbles are evenly-spaced and which ones are farther apart.			X				
grumble gap G2-3	The time passed between the end of the second grumble and the beginning of the third, measured from the spectrogram.			X				
# arches	The number of arches visible in the spectrogram. We define an arch as a parabola-shaped segment of a California ground squirrel warble where the frequency rises and then falls.			X				
arch-grumble gap	The time passed between the end of the last arch and the beginning of the first grumble, measured from the spectrogram.			X				
arch 1 duration	The time passed between the visible beginning of Arch 1 and the visible end of Arch 1, ignoring gaps in the arch.			X				
arch 2 duration	The time passed between the visible beginning of Arch 2 and the visible end of Arch 2, ignoring gaps in the arch.			X				
High frequency arch 1...n	The highest frequency in the F0 band of each arch, measured from the spectrogram.			X				
transition frequency arch 0/1, 1/2 …(n-1)/n	The low frequency at the junction between each of the arches, measured from the spectrogram. For the first arch, this is the low frequency at which it starts.			X				

# harmonics Arch 1…n	The number of visible harmonics in each arch.			X				
# subharmonics Arch 1…n	The maximum number of subharmonic bands appearing between any two main bands in the focal arch.			X				
Continuity % Arch 1…n	The estimated percentage of the focal arch that is visible in the spectrogram.			X				
F0 state	Qualitative assessment, later numerically coded, of the overall darkness of the F0 band.				X			
F1…Fn state	Qualitative assessment, later numerically coded, of the overall darkness of the focal band.				X			
F0 presence	Indicates whether the fundamental frequency band is visible in the spectrogram.					X		
Forked peaks	Indicates whether a spectrum slice taken at the instant of maximum amplitude contains forked (notched) peaks for each frequency band.					X		
# trill bursts	The number of individual notes (trill bursts) visible in the spectrogram.						X	X
loudest burst	The loudest trill burst in the call.						X	X
second loudest burst	The second-loudest trill burst in the call.						X	
# harmonics B1	The number of harmonic bands visible in the first trill burst.						X	X
entire F0 bandwidth B1	The bandwidth (frequency range) covered by F0 during the first trill burst, measured from the spectrogram						X	X
typical F0 bandwidth B1	The thickness (bandwidth) of the F0 band of the first trill burst, measured from a slice in the spectrogram where the burst is the most flat.						X	X
F0 ending low B1	The lowest frequency covered by F0 at the end of the first trill burst, measured from the spectrogram						X	X
F0 ending high B1	The highest frequency covered by the F0 band at the end of the first trill burst, measured from the spectrogram						X	X

burst duration B1	The time passed between the beginning of the first trill burst to the end of the first trill burst.						X	X
burst duration B2	The time passed between the beginning of the second trill burst to the end of the second trill burst.						X	
burst gap B1-2	The time passed between the end of the first burst and the beginning of the second burst.						X	X
burst gap B2-3	The time passed between the end of the second burst and the beginning of the third burst.						X	
gaps uniform	Indicates whether gaps between bursts appear uniform in length.						X	
larger gaps	Indicates which gaps between bursts appear longer than average.						X	
# snarfs	The number of snarfs visible in the call. We define a snarf as a low frequency broadband growl/snort. These only occurred in thirteen-liner calls.							X
chirp-click presence	Indicates whether the call contains a chirp-click. We define a chirp-click as a short harmonic burst in a thirteen-lined ground squirrel call that occurs before the main call and has a much lower F0 than the main call. These were uncommon.							X
snarf gap	The time passed between a snarf or chirp-click and the main call.							X

*Measured from F1 in black-tailed and F5 in white-tailed prairie dogs.

†Yellow-bellied marmot calls were measured by D. T. Blumstein and O. Munos. For methods, see Blumstein and Munos 2005 (ref. 14).

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