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Large Groups Breed Individuality

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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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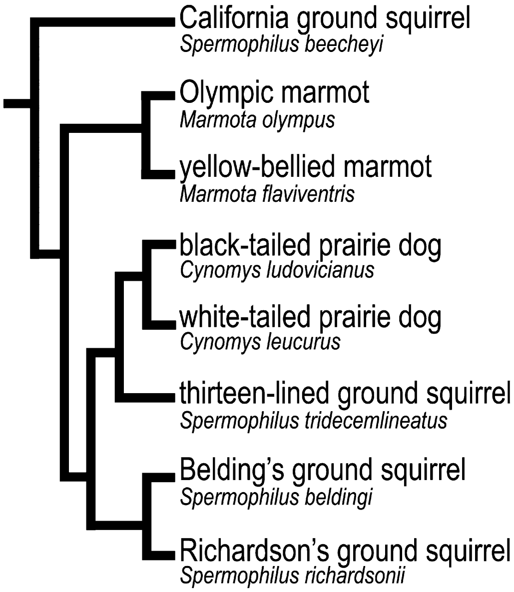

Figure 1. Phylogeny of Study Taxa

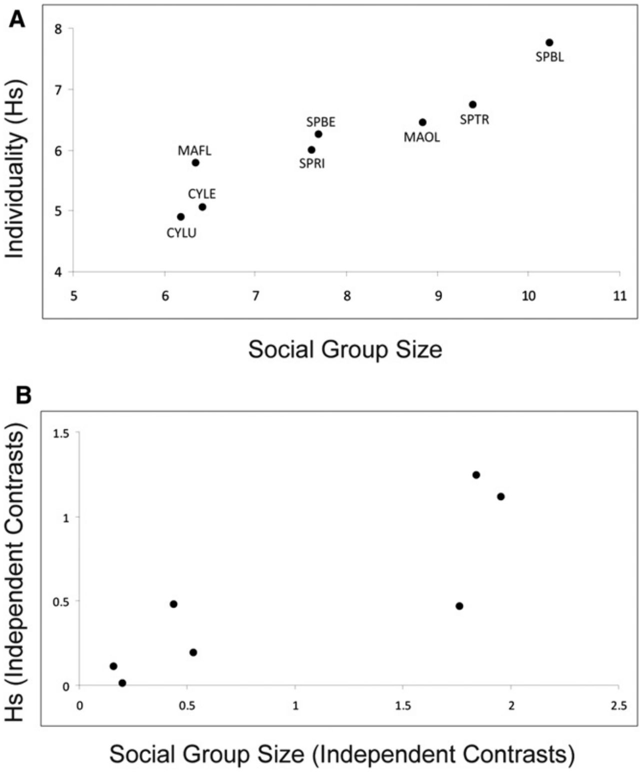

Figure 2. Social Group Size versus Vocal Individuality for Eight Species of Ground-Dwelling Sciurids

(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.

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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