Does Sociality Drive the Evolution of Communicative Complexity? A Comparative Test with Ground-Dwelling Sciurid Alarm Calls

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DOES SOCIALITY DRIVE THE EVOLUTION OF COMMUNICATIVE COMPLEXITY? A COMPARATIVE TEST WITH GROUND-DWELLING SCIURID ALARM CALLS

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Abstract.—While sociality has been hypothesized to drive the evolution of communicative complexity, the relationship remains to be formally tested. We derive a continuous measure of social complexity from demographic data and use this variable to explain variation in alarm repertoire size in ground-dwelling sciurid rodents (marmots, *Marmota* spp.; prairie dogs, *Cynomys* spp.; and ground squirrels, *Spermophilus* spp.). About 40% of the variation in alarm call repertoire size was explained by social complexity in the raw data set. To determine the degree to which this relationship may have been influenced by historical relationships between species, we used five different phylogenetic hypotheses to calculate phylogenetically independent contrasts. Less variation was significantly explained in contrast-based analyses, but a general positive relationship remained. Social complexity explained more variation in alarm call repertoire size in marmots, while sociality explained no variation in repertoire size in prairie dogs and no variation in phylogenetically based analyses of squirrels. In most cases, substantial variation remained unexplained by social complexity. We acknowledge that factors other than social complexity, per se, may contribute to the evolution of alarm call repertoire size in sciurid rodents, and we discuss alternative hypotheses. Our measure of social complexity could be used by other researchers to test explicit evolutionary hypotheses that involve social complexity.

While it is often implied that sociality drives the evolution of communicative complexity (e.g., Marler 1977; Waser 1982; Marler and Mitani 1988; Philips and Austad 1990; Hauser 1996), the hypothetical relationship is rarely explicitly stated, and the relationship has never been formally tested. Marler (1977, p. 46) predicted that "the richest elaboration of systems of social communication should be expected in intraspecific relationships, especially where trends towards increasing interindividual cooperation converge with the emergence of social groupings consisting of close kin." Waser (1982, p. 118) also linked sociality to communicative complexity when he noted "the value to a signaler of broadcasting information to recipients, and thus the degree to which selection favors specialized 'information-transfer' abilities, depend[s] on the social system." Testing the relationship between social complexity and communicative complexity requires explicit definitions of both variables in terms of complexity and comparative tests. In this article, we focus on the evolution of alarm call repertoire size in ground-dwelling sciurid rodents (marmots, *Marmota* spp.; prai-

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rie dogs, *Cynomys* spp.; and ground squirrels, *Spermophilus* spp.). We derive a continuous and objective measure of social complexity from demographic data and use this variable to explain variation in alarm call repertoire size.

Ground-dwelling squirrels are an ideal taxon to ask questions about the evolutionary impacts of social variation on communicative complexity. There is a large body of literature on social variety in marmots, prairie dogs, and ground squirrels (e.g., Murie and Michener 1984; Barash 1989; Hoogland 1995; Bibikow 1996). Social organizations range from those species that disperse immediately following weaning and live more or less solitary lives to those that exhibit delayed dispersal, in which overlapping generations of individuals share a home range and interact amicably. All ground-dwelling sciurids emit alarm calls, and repertoire size varies. Moreover, alarm calls are relatively common vocalizations and generally quite loud; estimates of repertoire size should be reasonably accurate. Thus, there is sufficient variation in both social organization and alarm call repertoire size for potential adaptive coevolution.

COMPLEXITY DEFINED

The term *complexity* is often used but rarely explicitly defined (McShea 1991). Others (e.g., Cole 1985) estimated behavioral complexity by counting the number of discrete behaviors. Simply put, the logic is that more discrete behaviors can be used more ways (Bonner 1988). While this definition may be a reasonable first approximation to estimating complexity, a richer definition of complexity implies more than simply counting the numbers of discrete behaviors. Complexity also implies some degree of variation or unpredictability in how elements (such as behaviors) are arranged (McShea 1991). Dawkins (1992, p. 265) presents a nice analogy to illustrate complexity. To compare the complexity of a lobster and an earthworm, write a book to describe each species. The longer book describes the more complex organism. All explicit definitions of complexity acknowledge that it must be viewed in a continuous fashion (e.g., Shannon and Weaver 1949; Sanders and Ho 1981; Cole 1985; Bonner 1988; McShea 1991). Thus, we must define sociality in a continuous way that reflects complexity.

Social Complexity

The evolution of sociality or social behavior is often studied by treating social variation categorically (e.g., Winston and Michener 1977; Prum 1994; Crespi 1996), and social systems are often classified in ways unrelated to complexity (e.g., Crook and Gartlan 1966; Wittenberger 1979; Armitage 1981; Croft 1989). Previous classifications that specifically acknowledged variation in complexity specified only a few somewhat subjective levels of complexity (e.g., Eisenberg et al. 1972). Colleagues have noted that perhaps complexity has little explanatory utility when thinking about social evolution because what ultimately matters is the relative fitness of different social structures, not complexity. We believe this is logical advice. But different social structures may result from differences in complexity, and/or complexity may be associated with different

social structures. Thus, complexity and social structure may be inseparable. If so, complexity is an objective measure of differences in social structure. Finally, and correctly or incorrectly, the evolution of complexity is a central theme in contemporary biology (Bonner 1988; McShea 1991, 1996; Szathmáry and Maynard Smith 1995). Thus, to study the relationship between social complexity and communicative complexity, we must explicitly define sociality in terms of complexity.

Group size is sometimes used as a measure of sociality (e.g., Eisenberg 1981; Janson and Goldsmith 1995). Yet social group size is an inadequate metric of social complexity because social behavior involves relationships between individuals, and the diversity of these relationships is not captured by simply using group size. Social behavior has been classified by the nature of the relationship (Alexander 1974), by the stability or persistence of the relationship (Foley and Lee 1989), by a species mating or grouping system (Wittenberger 1979; Wrangham 1986), by a series of ecological factors (Crook and Gartlan 1966), and by a series of life-history, ecological, and/or social variables (Clutton-Brock and Harvey 1977; Armitage 1981; Di Fiore and Rendall 1994). Because social behavior is typically defined categorically, it is not immediately obvious how to compare different social systems objectively with respect to variation in complexity. A new metric of social variation is required to specifically quantify complexity. This metric would ideally be broadly applicable to diverse taxa.

Previous classifications of primate, macropod, and ground-dwelling sciurid sociality subjectively classified species into social grades (e.g., Eisenberg et al. 1972; Armitage 1981; Michener 1983; Croft 1989). For sciurids, classification depended, in part, on the methods used and on available data. Michener (1983) classified species according to kinship and spatial distributions of different age and sex animals; for many species, detailed information on kinship and social structure was unavailable. The five social grades proposed in other works (Armitage 1981; Michener 1983) were not always congruent, and there was no obvious way to describe the continuous nature of sociality (i.e., variation within a social grade was ignored).

Classical information theory (Shannon and Weaver 1949) provides the tools to quantify complexity continuously and objectively. The number of binary digits (bits) required to describe a social system objectively defines social variation along a metric of complexity (also see Sanders and Ho 1981). In the communication literature, the Shannon-Wiener formula,

$$H(X) = -\sum p(i)\log_2 p(i), \tag{1}$$

defines the amount of potential information in a message, $H(X)$, given the relative frequency, $p(i)$, of a number of different signals, X_i. The variable $H(X)$ is the number of bits of information required to describe a communicative system with i different signals each occurring with a probability p. The simplest case is where there is a single signal given with 100% probability: $p(i) = 1$; $\log_2 p(i) = 0$. In this case, $H(X) = 0$, for no information is required to describe something that happened all the time. Analogously, if individuals always lived

alone, the species' social system would be very simple and would require few bits to be described fully.

To use information theory to describe social variation, we assumed that species with more demographic roles were more complex than those with fewer roles. A role is a "socially expected behavior pattern usually determined by an individual's status in a particular society" (*Webster's New Collegiate Dictionary,* 19th ed., s.v. "role"). For instance, two roles in a social group may be breeding and nonbreeding. Many types of roles change over time: nonbreeders may mature into breeders; breeders may not breed every year; subordinates may become dominants; a territory holder may become a floater; and so forth. Roles may also vary in their degree of specification: breeders and nonbreeders may be classified according to sex. Thus, a group may have both female breeders and female nonbreeders. Social structure can be described based on the roles present in a social group. Thus, some groups may have a single breeding male, no nonbreeding males, and a mix of breeding and nonbreeding females. Our use of the term *role* is very similar to Hinde's (1975) discussion of relationships. Sociality can be described by noting the nature and variety of relationships or, using our terminology, roles.

While it would be ideal to acknowledge the diversity and flexibility of roles present in social groups, such data are typically unavailable for many species, and more specific roles must emerge from demographic roles. We defined roles based on age and sex as reported in the literature, and we used social groups as the unit of analysis. For instance, some marmots had social groups containing adults, 2-yr-old and yearling nonbreeding individuals, and juveniles born that year. Some *Spermophilus* social groups had a single female with her young of the year. In all cases in which adult males and females lived together, we defined a role for adult males and a role for adult females. Our classification may oversimplify behavioral complexity. We do not intend our descriptions of complexity to be final; rather, we view them as the best possible given available information. The methodology permits us to quantify social complexity objectively and is amenable to the addition of new data.

We summarized the literature on the demographic structure of social groups and calculated an $H(X)$ for each role ($H(X)$adult males, $H(X)$adult females, etc.). Specifically, for each role, we counted the number of social group years (a social group studied for a year) that contained a particular number of individuals (e.g., 0, 1, 2, 3, . . . , n adult males, etc.) and used these counts to calculate each $H(X)$. The sum of all the $H(X)$'s for a given species, $H(X)_t$, was the total number of bits required to describe the social structure of that species. However, $H(X)_t$ alone does not acknowledge kin structure. Envision two social systems with exactly the same $H(X)_t$ but differing in kinship. Because kinship adds new dimensions to social relationships, we would like those social groups with kinship to be more complex than those without kinship. One possible way to do this that is amenable to comparative study would be to incorporate the time to natal dispersal. There is variation in the time to natal dispersal among ground-dwelling sciurids that generates kin structure in social groups. To incorporate the added complexity of kin structure created by delayed dispersal, we multiplied

each $H(X)_t$ by a number reflecting the time to natal dispersal, T_{nd}. Species that dispersed before their first hibernation or during their first active season were multiplied by 1, species that dispersed before their second hibernation or during their second active season were multiplied by 2, and species that dispersed after their second hibernation or active season were multiplied by 3. In doing so, we are aware that sciurids with more demographic roles also have delayed dispersal. Other taxa may increase social complexity solely by immigration and not by delayed dispersal. While we intend this metric to be generalizable to other taxa, we are aware that we further increase the social complexity for complex species by multiplying $H(X)$ by T_{nd}. For our 22 species, this multiplication has only small effects on the relative positions in the social ranking; $H(X)_t$ and SC_d are highly correlated ($r_s = 0.92$, $P < .001$). Only *Spermophilus columbianus,* generally considered to be moderately social (Armitage 1981; Michener 1983), markedly increased its social ranking as a consequence of incorporating T_{nd} into the calculation of SC_d. Thus, this multiplication acknowledges, and emphasizes, the potential importance of kin structure. We log-transformed all values for analysis. Our measure of social complexity calculated from demographic data, SC_d, was

$$SC_d = \log[(H(X)_t)T_{nd}]. \quad (2)$$

An information theory approach emphasizes intraspecific variation when defining social variability. This makes sense intuitively: species for which there is variation in the number of possible age/sex classes living together must be more socially flexible than those in which the number of age/sex classes living together remains fixed. For many social species, social flexibility is the norm (Lott 1991). Moreover, variability is the essence of what is typically emphasized in discussions of complexity (McShea 1981). Theoretically, emphasizing variation can lead to the strange result in which a demographic role (e.g., adult females) in which half the animals lived alone and the other half lived with one other animal would have the same $H(X)$ as a species in which half the individuals lived with five animals and the other half lived with 10 animals. This appeared not to be a problem in our sciurid data set.

At some point in the future, we may be able to define roles according to dominance status or according to types of affiliative behaviors or relationships between animals (e.g., Lee 1994). Presently, comparative data are lacking to do so, and we resorted simply to defining age/sex roles. This categorization provides an estimate of the types of social interactions possible; social interactions must emerge from animal grouping patterns (e.g., an asocial species does not allogroom much). Because demographic data were often lacking on sex ratios of subadults, only adults had two roles; juveniles, yearlings (when present), and 2-yr-olds (when present) had a single role each.

Communicative Complexity

Information theory can explicitly be used to describe and quantify communicative complexity. Unfortunately, to use information theory properly, we must study both the production and perception of signals; not all forms of acoustic variation may be perceptually salient (e.g., Green and Marler 1979; Hauser

1996). Information on both the production and perception of signals is practically unavailable for the vast majority of species and only for a few sciurids. Thus, we use repertoire size, a variable more amenable to comparative study, as a first approximation of communicative complexity. We focused on alarm call repertoire size.

When alarmed by predators, many species produce specific vocalizations (Klump and Shalter 1984). We believe that alarm call repertoire size is an ideal system to study the relationship between social and communicative complexity for the following reasons. First, alarm calls are social calls. Alarm calling may increase direct or indirect fitness components (e.g., Dunford 1977*b;* Sherman 1977; Schwagmeyer 1980; Shields 1980; Blumstein et al. 1997), and thus social complexity may drive the evolution of alarm call complexity.

Second, ground-dwelling sciurid alarm calls tend to be loud and obvious; thus, counts of alarm repertoire size should not be biased toward the better-studied species. In contrast, those species studied in captivity and/or those species well studied in the field are routinely reported to produce more nonalarm vocalizations than less well studied species (e.g., Waring 1970). Nonalarm vocalizations tend to be quieter and are often less obvious to observers (D. T. Blumstein, personal observations). This systematic bias that prevents a meaningful comparison of ground-dwelling sciurid total repertoire size is not present when comparing alarm repertoire size.

Third, each alarm call tends to be a relatively short duration vocalization that primarily functions on an immediate timescale to potentially alert conspecifics (e.g., Sherman 1977; Schwagmeyer 1980; but see Schleidt 1973; Owings and Hennessy 1984; Loughry and McDonough 1988; D. T. Blumstein, unpublished data, for examples of calls functioning on a longer timescale). In contrast, many songbirds combine unique acoustic elements into more elaborate songs that function on a longer timescale and for different functions. For instance, bird songs may identify territories, signal readiness to mate, and so forth (Catchpole and Slater 1995). When acoustic elements are combined to function on a longer timescale, it is much more difficult to estimate repertoire size (Kroodsma 1982).

Fourth, while social signals used in other situations should logically co-vary with social complexity (e.g., aggressive and/or submissive signals), many of these signals are multimodal (e.g., an aggressive dog may growl and erect its hair), and it is difficult simply to describe multimodal signal (their systematic study is in its relative infancy; see, e.g., Hughes 1996). Moreover, while olfactory signals may be an important component of multimodal signals, estimating the size of an olfactory repertoire is difficult. Because alarm calls are loud and obvious acoustic signals, estimates of repertoire size should be less biased.

Finally, whereas environmental experience influences song repertoire size in several bird families, repertoire size in mammals seems much less plastic (e.g., Snowdon 1982; Snowdon and Elowson 1992; Hauser 1996), and there is no evidence that any species learns its alarm calls. Together, these factors make mammalian alarm calls make an ideal system to study the relationship between social and communicative complexity.

Some species vary calls according to the degree of risk the caller experi-

ences—perhaps according to the response urgency, or the imminence of predation that the caller faces (Robinson 1981; Owings and Hennessy 1984; Blumstein 1995*a;* Blumstein and Armitage 1997). In addition, some species vary call structure according to the type of predator detected (Seyfarth et al. 1980; Davis 1984; Cheney and Seyfarth 1990; Marler et al. 1992; Macedonia and Evans 1993). Identifying predator-specific calls is important, for it was generally assumed that only humans could communicate about events and stimuli external to themselves; nonhumans supposedly only communicated about their internal states (reviewed in Marler 1985; Hauser 1996). Regardless of whether calls are predator specific or not, both types of variable alarm calls are referred to as situationally specific in that call structure in some way varies according to situation.

Repertoire size should limit the degree to which risk or predator type can be specified. Thus, repertoire size should be associated with the potential benefits an individual hearing a given alarm call can gain by hearing that call. For instance, if a species has an ''eagle'' call and a ''fox'' call, an individual hearing an eagle call ''knows'' that there is a predator in the air and thus may take appropriate action. In contrast, for species that communicate the degree of risk a caller experiences, a ''high-risk'' call initially conveys information only about the caller's perception of risk. Thus, a perceiver would presumably require additional contextual information (Leger 1993)—such as the caller's location, the caller's age, the caller's identity, or the caller's concomitant behavior—to interpret properly the degree of risk the caller experienced and thus the degree of risk the perceiver may experience. It is likely that more complex kin-structured social systems will select for more complex alarm communication. Specifically, we predict that social complexity will select for larger repertoire size because larger repertoires permit situational variation to be more precisely specified.

METHODS

The Data Set

We reviewed the literature for studies that reported demographic information and for studies that discussed alarm communication. A number of studies did not report litter size distribution. If a mean and standard deviation were reported, we assumed litter size was normally distributed to estimate litter size distribution. We either chose the single best demographic data set (e.g., Hoogland 1995) or combined several studies. When different studies contributed demographic data, we weighted the average by sample size. We counted the number of discrete call types to calculate alarm call repertoire size. Our counts may overestimate call repertoire size for species in which call types continuously graded into each other, if and when previous investigators reported continuously varying calls as discrete call types. Our counts may underestimate call repertoire size for species that vary the acoustic microstructure of their calls with predator type (e.g., C. Slobodchikoff, personal communication; see the double-daggered note

TABLE 1

FINAL COMPARATIVE DATA SET AND SOURCES CONSULTED

Species	T_{nd}	$H(X)_t$	SC_d	N AC	References Consulted*
Marmota flaviventris	2	5.70	1.06	2†	1–5
Marmota caligata	3	7.42	1.35	4	6–9, 17
Marmota olympus	3	9.62	1.46	4	10, 17
Marmota camtschatica	3	4.18	1.10	1	11–13
Marmota monax	1	1.88	.27	1	14–17, 78, 79
Marmota caudata	3	5.59	1.22	1	17–20
Marmota marmota	3	8.57	1.41	2	21–26
Cynomus ludovicianus	2	6.60	1.12	1	27–29
Cynomus parvidens	2	8.52	1.23	1	30, 31
Cynomus gunnisoni	2	5.32	1.03	1‡	29, 32–34
Cynomus leucurus	1	6.84	.84	1	29, 35
Spermophilus tereticaudus	1	3.00	.48	1	36–40
Spermophilus tridecemlineatus	1	3.16	.50	1	41–48
Spermophilus lateralis	1	2.39	.38	2	49–51
Spermophilus beecheyi	1	1.83	.26	2§	52–55
Spermophilus variegatus	1	2.67	.43	2	56–60
Spermophilus armatus	1	2.76	.44	2	61–63
Spermophilus beldingi	1	2.52	.40	2	64–66
Spermophilus richardsonii	1	2.45	.39	3	67, 68
Spermophilus elegans	1	2.70	.43	2	67–70
Spermophilus columbianus	2	2.23	.65	3	67, 71–74
Spermophilus townsendii	1	2.55	.41	2	75–77

NOTE.—Variables: T_{nd} = the time to natal dispersal where 1 = disperses during first active season or before first hibernation, 2 = disperses during the second active season or before second hibernation, and 3 = disperses after second active season/hibernation; $H(X)_t$ = sum of $H(X)$ for each demographic "role" present; SC_d = our measure of social complexity calculated from demographic data; and N AC = the number of alarm calls.

* 1, K. B. Armitage, unpublished data; 2, Armitage 1991; 3, Frase and Hoffmann 1980; 4, Blumstein and Armitage 1997; 5, Waring 1966; 6, Barash 1974; 7, Barash 1980; 8, Holmes 1979; 9, Holmes 1984; Barash 1973; 11, Kapitonov 1963 cited in Rausch and Rausch 1971; 12, Mosolov and Tokarsky 1994; 13, Ognev [1947] (1963); 14, de Vos and Gillespie 1960; 15, Ferron an Ouellet 1989; 16, Meier 1985; 17, D. T. Blumstein, unpublished data; 18, Blumstein and Arnold, in press; 19, Blumstein 1995*a;* 20, Blumstein 1995*b;* 21, Arnold 1993*a;* 22, Arnold 1993*b;* 23, Barash 1976; 24, Blumstein and Arnold 1995; 25, Perrin et al. 1993*b;* 26, Perrin et al. 1993*a;* 27, Hoogland 1995; 28, King 1955; 29, Waring 1970; 30, Pizzimenti and Collier 1975; 31, Wright-Smith 1978; 32, Fitzgerald and Lechleitner 1974; 33, Rayor 1985; 34, Rayor 1988; 35, L. Cooke, personal communication to K. B. Armitage; 36, Dunford 1977*b;* 37, Dunford 1977*c;* 38, Dunford 1977*a;* 39, Ernest and Mares 1987; 40, Reynolds and Turkowski 1972; 41, Matocha 1977; 42, McCarley 1966; 43, Rongstad 1965; 44, Schwagmeyer 1980; 45, Schwagmeyer and Brown 1981; 46, Schwagmeyer and Brown 1983; 47, Streubel and Fitzgerald 1978; 48, Wistrand 1974; 49, Bartels and Thompson 1993; 50, Hatt 1927; 51, Phillips 1981; 52, Evans and Holdenreid 1943; 53, Fitch 1948; 54, Leger et al. 1980; 55, Owings et al. 1977; 56, Krenz 1977; 57, Oaks et al. 1987; 58, Ortega 1990; 59, Ortega 1991; 60, Shriner and Stacey 1991; 61, Balph and Balph 1966; 62, Balph and Stokes 1963; 63, Slade and Balph 1974; 64, Morton and Gallup 1975; 65, Robinson 1981; 66, Turner 1973; 67, Koeppl et al. 1978; 68, Michener 1979; 69, Pfeiffer 1982; 70, Zegers 1984; 71, Betts 1976; 72, Festa-Bianchet and King 1991; 73, Harris et al. 1983; 74, Zammuto and Millar 1985; 75, Smith and Johnson 1985; 76, Rickart 1986; 77, Rickart 1987; 78, Hamilton 1934; 79, Lloyd 1972.

† Yellow-bellied marmots produce three vocalizations in potentially alarming situations but only two of them (whistles and trills) are loud alarm calls (Blumstein and Armitage 1997). Moreover, the quiet call (chucks), when played back, does not elicit an alarm response in conspecifics. For these analyses, we scored yellow-bellied marmots as having two-alarm vocalizations.

‡ The microstructure (specifically, the shape of certain harmonics) of Gunnison prairie dog alarm barks co-varies with predator species (C. Slobodchikoff, personal communication) and with the identity of some individual predators (Slobodchikoff et al. 1991). It is interesting that variation appears continuous: for this analysis, we scored Gunnison prairie dogs as having a single-alarm vocalization (barks).

§ Owings and Leger (1980) found microstructural predator and social specificity in California ground squirrels' chatter vocalization, and Leger et al. (1980) found microstructural variation in socially elicited single-note vocalizations. For this analysis, we scored California ground squirrels as having two alarm vocalizations: chatters and single-note vocalizations.

in table 1). Because not all species were studied with equivalent detail, we focused on the number of discrete alarm call types.

Regression Analyses

We regressed our measure of social complexity against alarm call repertoire size where we set the *y*-intercept to 1.0 because all species had at least one alarm call and we expected repertoire size to increase with complexity. To control for possible phylogenetic nonindependence on alarm repertoire size and on sociality, we examined the relationship using standardized independent contrasts calculated for each variable. We used Purvis and Rambaut's (1995) statistical package, CAIC, to calculate independent contrasts for social complexity and alarm call repertoire size. As specified in the CAIC manual, we regressed these standardized contrasts through the origin. In all cases, we used one-tailed tests because we have a specific directional hypothesis.

There is no published phylogenetic hypothesis that includes all species of interest, and different species groups have been studied at various degrees of detail. We eagerly anticipate the publication of inclusive and well-supported phylogenetic hypotheses. In their absence, we generally inferred phylogeny from taxonomy (Nowak and Paradiso 1983) but added additional information where known (Howell 1915; Hoffmann and Nadler 1968 for the marmots; Hafner 1984 for sciurid subgenera), and we refer to this tree as tree 1 (fig. 1). Black (1972) assumed that the genus *Marmota* evolved in the New World from a woodchuck-like ancestor. We switched the location of *Marmota marmota* and *Marmota monax* to create tree 2 (fig. 1). Thomas and Martin (1993) questioned the ancestral location of the genus *Marmota.* They suggested the genus *Marmota* evolved recently from *Spermophilus* ancestors. We calculated independent contrasts from a tree, tree 3 (fig. 1), in which *Cynomys, Marmota,* and the remaining *Spermophilus* subgroups branch simultaneously, and a tree, tree 4 (fig. 1), that reflects the recent origin of marmots. We generated tree 5 (fig. 1) to recognize evidence suggesting *Cynomys* is the crown group of the subgenus *Spermophilus* in the currently recognized genus *Spermophilus* (Dobson 1985 and references therein; Goodwin 1990).

To calculate standardized independent contrasts, we set all branch lengths equal and selected the crunch option in CAIC. Setting branch lengths equal assumes an underlying evolutionary model of punctuational change (e.g., Harvey and Pagel 1991) and is less inaccurate than estimating branch lengths with missing species (Purvis and Rambaut 1995). No independent measures of branch length are available for our partial phylogenies, so we did not calculate contrasts assuming Brownian motion trait evolution.

There was variation in the repertoire size of marmots and ground squirrels but not prairie dogs (Results). For marmots alone and for ground squirrels alone, we regressed social complexity against alarm call repertoire size and reran regressions on independent contrasts calculated from the relevant trees (two trees for marmots and four trees for squirrels). Finally, because the squirrel distinction may be artificial (e.g., Dobson 1985), we reran regressions with a data set containing *Cynomys* and *Spermophilus.*

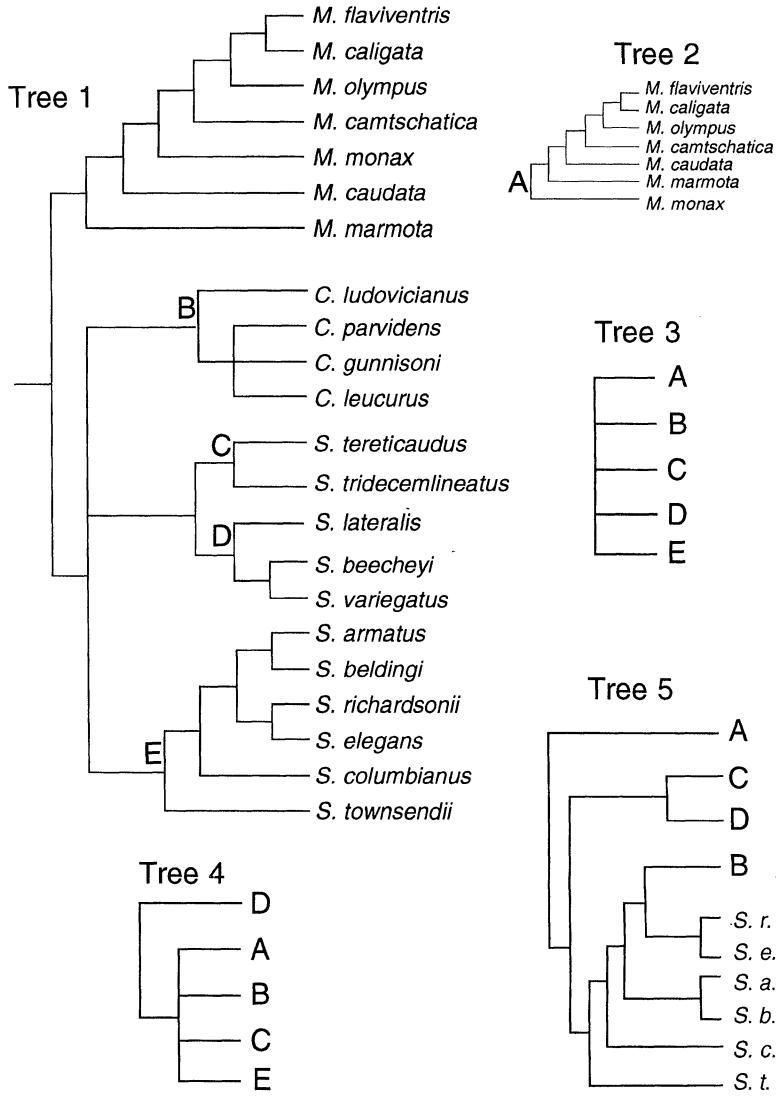

FIG. 1.—Phylogenetic hypotheses used to calculate contrasts. These are partial working phylogenies of sciurid rodents; recognized genera and species not included in these analyses are not illustrated. *Tree 1,* A taxonomically derived tree with phylogenetic information added where known. *Tree 2, Marmota monax* shifted to reflect its possible ancestral location in *Marmota*. Letters marked at higher nodes on trees 1 and 2 are used to illustrate the structure of the following two trees. *Tree 3,* An unresolved origin of *Marmota. Tree 4,* A recent origin of *Marmota* and other sciurids from a subgroup of species currently classified as *Spermophilus. Tree 5, Cynomys* as the crown group of the subgenus *Spermophilus.*

In addition to calculating independent contrasts, we also analyzed the data using phylogenetic autocorrelation (Cheverud et al. 1985; Gittleman and Kot 1990; Gittleman and Luh 1992). Phylogenetic autocorrelation permitted us to estimate and statistically remove the maximum amount of variation in each variable (social complexity, repertoire size) that could be explained by phylogenetic similarity. Phylogenetic autocorrelation assumes explicitly statistical models of trait change that vary according to an autoregressive model (Purvis et al. 1994; Martins 1995) and, under a Brownian motion model of evolution, may produce erratic results with sample sizes <40 (Martins 1996). We used a single phylogenetic hypothesis, the taxonomy reported in Nowak and Paradiso (1983), to estimate the phylogenetic distance matrix. The phylogenetic distance matrix defines the sets of species with which each individual species' trait value will be compared to search for autocorrelation. The classical taxonomic classification recognizes subgenera in both *Cynomys* and *Spermophilus* and recognizes two subtribes: one containing *Marmota* and the other containing both *Cynomys* and *Spermophilus*. We used the program P.A. (Luh et al. 1995) to fit phylogenetic autocorrelations. Correlograms (plots of Moran's *I*—the autocorrelation statistic—vs. phylogenetic distance) suggested significant phylogenetic autocorrelation at lower taxonomic levels that disappeared after we calculated phylogeny-free residuals. We regressed the phylogeny-free residuals against each other to estimate the variation in alarm repertoire size independently explained by social complexity.

RESULTS

Our final comparative data set contained data for 22 species: seven of 14 marmots (three Old World, four New World), four of five prairie dogs (a New World genus), and 11 of 38 ground squirrels (all were New World species; table 1). Our metric of social complexity was highly correlated with two previous indexes of sciurid sociality ($r = 0.84$, $N = 17$ [Armitage 1981]; $r = 0.89$, $N = 17$ [Michener 1983]). Nevertheless, there are some discrepancies with less objective assessments of social complexity. For instance, J. Hoogland (personal communication) noted that our demography-based metric classified black-tailed prairie dogs (*Cynomys ludovicianus*) as less complex than Utah prairie dogs (*Cynomys parvidens*). His detailed behavioral observations suggest that black-tailed prairie dogs engaged in more types of social behavior than Utahs. It is interesting that many of black-tailed prairie dogs' social interactions during the time before pups emerge are related to perpetrating or preventing infanticide. It would be interesting to study the relationship between social complexity and the amount and/or degree of amicable behaviors. Despite this exception (black-tailed vs. Utah prairie dogs), our metric generally is consistent with our expectations based on previous studies.

Social complexity varied between genera (Kruskal-Wallis $P = .004$). Post hoc multiple comparisons ($P < .05$) suggested marmots and prairie dogs were more complex than ground squirrels. Alarm call repertoire size tended to vary between genera (Kruskal-Wallis $P = .055$); prairie dogs had significantly fewer

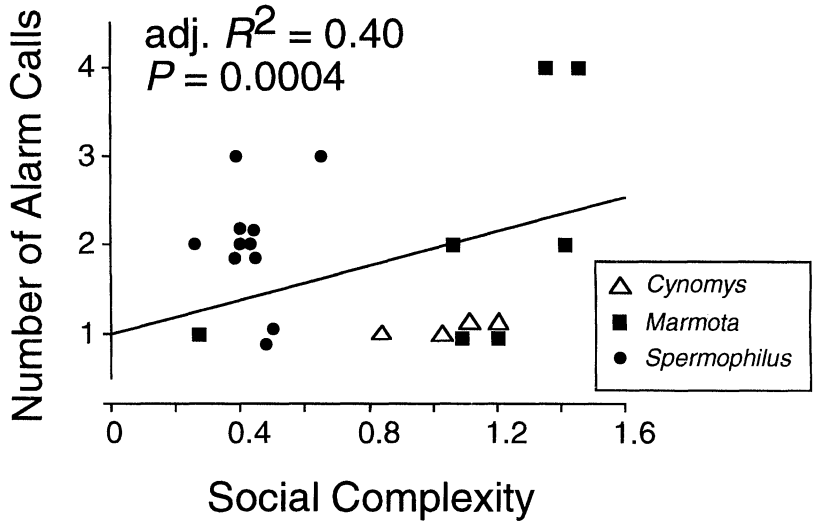

FIG. 2.—The relationship between social complexity and alarm call repertoire size. Because all species had at least one alarm call, we set the y-intercept at 1. Overlapping values are vertically offset; the P value is one-tailed.

TABLE 2

VARIATION IN ALARM CALL REPERTOIRE SIZE EXPLAINED BY SOCIAL COMPLEXITY (ADJUSTED R^2) ASSUMING FIVE DIFFERENT EVOLUTIONARY SCENARIOS

	Tree 1	Tree 2	Tree 3	Tree 4	Tree 5
All data	6.5*	7.9*	11.9*	10.6*	30.6†
No woodchucks	3.8 NS	5.1*	5.2 NS	10.4*	20.5**
Marmots only	17.3*	18.5*	...	...	...
Marmots without woodchucks	77.7†	73.6†	...	...	...
Squirrels only	0 NS	0 NS	0 NS	0 NS	...
Cynomys and *Spermophilus*	...	...	...	...	0 NS

NOTE.—NS = $P > .1$ (one-tailed).
* $.1 > P > .05$ (one-tailed).
** $.05 > P > .01$ (one-tailed).
† $.01 > P > .001$ (one-tailed).

vocalizations than did either marmots or ground squirrels. About 40% of the variation in alarm repertoire size was significantly explained (adjusted R^2 = 0.40, P = .0004) by SC_d, our measure of social complexity (fig. 2). After controlling for possible phylogenetic effects by calculating independent contrasts, we found that social complexity explained less variation in alarm call repertoire size (table 2). Under some evolutionary scenarios, no significant variation in repertoire size was significantly explained by social complexity. Regression on phylogeny-free residuals calculated from the phylogenetic autocorrelation analy-

sis generated positive results; once again, less variation was explained after removing phylogenetic effects (adjusted $R^2 = 11.6$, $P = .031$).

Woodchucks (*Marmota monax*) were an outlier that had a large impact on some results of the phylogenetic analyses. Woodchucks are a marmot with a simple social system and apparently a single, two-part alarm call (Hamilton 1934; Lloyd 1972; Meier 1985). We have been trying to study woodchuck alarm communication in detail to no avail: in over 100 h of fieldwork on woodchuck alarm communication, not a single alarm call was heard (D. T. Blumstein, unpublished data). Given some uncertainty about the number of alarm vocalizations woodchucks produce (one or two), we removed woodchucks from the analysis and recalculated all contrasts. Removing woodchucks reduced the amount of explained variation (table 2).

When marmots and squirrels (prairie dogs do not have variable numbers of alarm vocalizations) were analyzed separately, results were similar. About 54% of the variation in marmot repertoire size was explained by our measure of social complexity ($P = .01$), and significant variation was explained after calculating independent contrasts to control for phylogenetic effects under some evolutionary scenarios (table 2). When we examined the effect of social complexity on alarm repertoire size in marmots alone, removing woodchucks greatly increased explained variation. About 69% of the variation in ground squirrel repertoire size was explained by social complexity ($P = .0003$), while no significant variation was explained after controlling for potential phylogenetic similarity using independent contrasts given any of the evolutionary scenarios. Finally, when we combined *Cynomys* and *Spermophilus,* about 18% of the variation in repertoire size was explained in the raw data set ($P = .0293$), while no significant variation was explained in the contrast-based analysis (table 2). The phylogenetic autocorrelation estimated that 54% of the variation in social complexity was attributable to phylogenetic (specifically taxonomic) similarity, while only 4% of the variation in alarm call repertoire size in analyses that included woodchucks and 6% of the variation in analyses that excluded woodchucks were attributed to phylogenetic similarity. Thus, substantial variation in alarm call repertoire size remained unexplained and was potentially available for adaptive coevolution with social complexity.

DISCUSSION

Complex social behavior explained some, but not most, of the variation in alarm repertoire size in sciurid rodents. Because both vocalizations (e.g., Nikolskii 1976; Macedonia and Stanger 1994; but see Nottebohm 1975; Irwin 1990) and social behavior (e.g., Edwards and Naeem 1993; Di Fiore and Rendall 1994; Prum 1994; Chan 1996; but see Gittleman et al. 1996) may have substantial phylogenetic information, we adjusted for and/or removed the effects of phylogenetic similarity. Given some uncertainty in historical relationships, we examined several alternative phylogenetic hypotheses. The specific hypothesis we used influenced the amount of explained variation, but the general relationship remained positive. When we examined subsets of the full data set, we found that

after accounting for phylogeny, social complexity may (in *Marmota*) or may not (in *Spermophilus* and *Cynomys*) be an important determinant of communicative complexity. Closely related squirrels tended to have similar numbers of alarm calls, and there is relatively limited variation in both SC_d and the number of alarm calls to explain. In contrast, marmots had the most variation in both SC_d and the number of alarm calls to be potentially explained.

If social behavior is not the primary determinant of alarm repertoire size in sciurids, what else might be responsible for the evolution of complex communication? At least four factors other than sociality may generally influence the evolution of complex communication and specifically influence the evolution of alarm call complexity. We do not suggest that these (and potentially other) factors are equally important in the evolution of complex communication. However, they might explain additional unexplained variation in communicative complexity.

Variation in the facial or laryngeal morphology may constrain or permit the production of variable alarm calls or other vocalizations (Fitch and Hauser 1995; Hauser 1996). While this may account for variation among genera, within a genus animals appear superficially similar. Detailed morphological studies ultimately need to determine whether there are differences within or between genera. As a first approximation, one reason to study communicative complexity in sciurids is the ability to discount the importance of within-genus morphological variation.

Physical and/or biological habitat acoustics may directly influence communicative complexity and may also interact with social behavior. Sounds must be transmitted through space during which time they may degrade in several ways and/or attenuate (Morton 1975; Wiley and Richards 1978; Brown and Waser 1988; Forrest 1994). In particularly destructive environments, effective communication may have to be simple. If habitat structure precludes differentiation of two sounds from each other at a distance (e.g., marmot example in Blumstein and Daniel, in press), the physical habitat has effectively selected for relatively simple communication. The biological habitat may be defined as the suite of other vocally communicating animals. With others present, available ''bandwidth'' may be limited and acoustic structure may be constrained (Ryan 1988). Competition with other conspecifics may select for greater acoustical structural variation (Alexander 1960). Both forms of habitat acoustics may interact with social behavior. Certain physical environments may have certain types or distributions of resources and may favor certain social systems (Wittenberger 1981). If certain types of habitats also have specific acoustics, then effective communication may require individuals to clump. Animals living in habitats with considerable acoustic competition may also compete with heterospecifics for bandwidth in which to communicate (Ryan 1988). Alternatively, mutualistic alarm-calling relationships with other species (e.g., Waring 1966; Rasa 1983; Seyfarth and Cheney 1990) may influence the costs and benefits of associating with other conspecifics and may constrain acoustic variation.

Finally, specific needs may influence communicative complexity and/or interact with social behavior. For instance, one compelling hypothesis for the evolu-

tion of predator-specific alarm calls is that species with fundamentally different predator-specific escape strategies will benefit most from predator-specific calls (Macedonia and Evans 1993). For example, vervet monkeys (*Cercopithicus aethiops*) produce acoustically different calls in response to different types of predators; they chutter to snakes, bark to leopards, and cough to eagles (Cheney and Seyfarth 1990). Monkeys hearing chutters immediately stand bipedally and look for snakes, those hearing barks climb trees and retreat to the distal part of limbs where they will be safe from leopards, and those hearing coughs retreat to the center of trees where they are safe from eagles. Macedonia and Evans (1993) predicted that species with predator-specific escape strategies, like vervet monkeys, will have predator-specific alarm calls. Because there is variation in sciurid predators, some species may have predator-specific escape strategies, and the incompatibility of these strategies may be associated with larger repertoire sizes. However, because most ground-dwelling sciurids flee to a burrow when alarmed, their behavior may reduce selection for predator-specific escape strategies. The need to avoid predators may influence how conspecifics are distributed in space, which in turn may influence social behavior.

More data and better phylogenetic resolution will likely permit a more exact estimate of the variation in alarm call repertoire size explained by social complexity. Yet because alarm repertoires may be simultaneously influenced by several other causal factors, future analyses should simultaneously study the relative importance of these other factors. Thus, we suggest the question be rephrased: How important is social complexity, relative to other causal factors, for the evolution of communicative complexity?

Current evidence suggests the genus *Marmota* may offer a good opportunity for future research. The relationship between alarm call repertoire size and social complexity is significant when controlling for phylogenetic effects. Marmots vary in both alarm call repertoire size and in SC_d more than either ground squirrels or prairie dogs. Thus, we suggest that studying additional species of marmots is an efficient way to address the question of the relative importance of social complexity and other causal factors in the evolution of complex communication. Alternatively, another research agenda might focus on the currently recognized genus *Spermophilus* because there is a relatively high alarm call complexity in spite of limited social complexity. Thus, it should be possible to identify factors other than sociality that influence communicative complexity.

In the future, we hope investigators will publish more specific data on age/sex distributions of other taxa to permit the study of complexity in other taxa. However, many socioecological questions are studied by comparing populations of a single species living in different ecological settings. While we used our metric of complexity to study variation among species, future investigators could use it to study intraspecific variation in complexity.

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