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Review

Evolving communicative complexity: insights from rodents and beyond

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Social living goes hand in hand with communication, but the details of this relationship are rarely simple. Complex communication may be described by attributes as diverse as a species' entire repertoire, signallers' individualistic signatures, or complex acoustic phenomena within single calls. Similarly, attributes of social complexity are diverse and may include group size, social role diversity, or networks of interactions and relationships. How these different attributes of social and communicative complexity co-evolve is an active question in behavioural ecology. Sciurid rodents (ground squirrels, prairie dogs and marmots) provide an excellent model system for studying these questions. Sciurid studies have found that demographic role complexity predicts alarm call repertoire size, while social group size predicts alarm call individuality. Along with other taxa, sciurids reveal an important insight: different attributes of sociality are linked to different attributes of communication. By breaking social and communicative complexity down to different attributes, focused studies can better untangle the underlying evolutionary relationships and move us closer to a comprehensive theory of how sociality and communication evolve.

Keywords: sociality; individuality; repertoire size; alarm call; information theory; vocal complexity

1. WHAT IS COMPLEXITY?

While most of us have an intuitive idea of what constitutes complexity, complexity is difficult to define [1]. A system is typically considered more complex if it contains more parts, more variability or types of parts, more connections or types of connections between parts or more layers of embedded meaning. The information [2] required to describe a system can be thought of as a measure of the system's complexity ('Kolmogorov complexity', after [3]). To illustrate, Dawkins [4, p. 265] provides a simple thought experiment: when comparing two items or systems, imagine writing a book to describe each one. The longer book will describe the more complex system. Information-based definitions of complexity are most useful because they allow complexity to be quantified and compared with a single metric [5].

Social complexity can be defined in numerous ways (e.g. the number of individuals [6–8], the number of demographic or social roles [9,10], the strength of social bonds [11–13], the complexity of group sub-structure and relationships [14–18] and combinations of these [19,20]). Each of these definitions can be considered an attribute of sociality. What these definitions have in common is they quantify social complexity via the number or variability of the social system's parts, connections or layers of categorization (table 1).

One integral attribute of social complexity is perhaps the most straightforward: social group size. The number of individual animals present in a social group influences that group's resource needs [21], disease ecology [22] and predation risk [23]. Furthermore, social group size defines boundaries for other attributes of social complexity, such as mating systems or social networks [24]. Group size also directly affects the communicative landscape, since more individuals may be communicated with, followed, discriminated or ignored [5,25–27]. Social group size is often straightforward to quantify. If a social group's boundaries are well defined, then a simple head count is all that is needed. For all these reasons, it is not surprising that social group size is one of the most commonly studied attributes of social complexity and has been used in a variety of taxa [7,28–38].

Another critical attribute of social complexity is the number or variability of social roles in a social group. A role can be thought of as a socially expected behavioural pattern. For instance, social roles may be based on whether an individual is a dominant or subordinate, a producer or scrounger, or a breeder or non-breeder. Blumstein & Armitage [39] quantified social roles by focusing on demographic (age/sex) roles in social groups, which can be quantified using information theory. The key assumption was that groups with more overlapping generations, and those with more age-sex classes present, were more socially complex in their demographic roles.

Complexity in communication can be defined analogously to complexity in sociality, i.e. via the number or

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One contribution of 13 to a Theme Issue 'The social network and communicative complexity in animals'.

Table 1. A selection of attributes of social systems and communication systems that can vary in complexity. The categories suggested here are neither mutually exclusive nor exhaustive, and no causal relationships are implied.

	number of system parts	types of system parts	connections between parts	layers of structure, categorization or meaning	openness and variability
social complexity	group size social group size colony, aggregation, or community size group size	roles social demographic reproductive	social bonds may be quantified with social network statistics and may be agonistic or affiliative matriline structures social hierarchies territorial neighbour networks	group substructure matrilines coalitions group superstructure fission–fusion group aggregations post-dispersal ties	fluidity or variability of social attributes group membership social hierarchies reproductive roles
communicative complexity	repertoire size (within a signal type) entire repertoire repertoire within an age class, sex or situational context	repertoire size (across signal types)	syntax connections between signals	referential and functionally referential communication communication of signal urgency or signaller's affective state embedded signature information signaller's age, sex, condition or individual identity	learning and modification of signals openness of signal repertoires and syntax

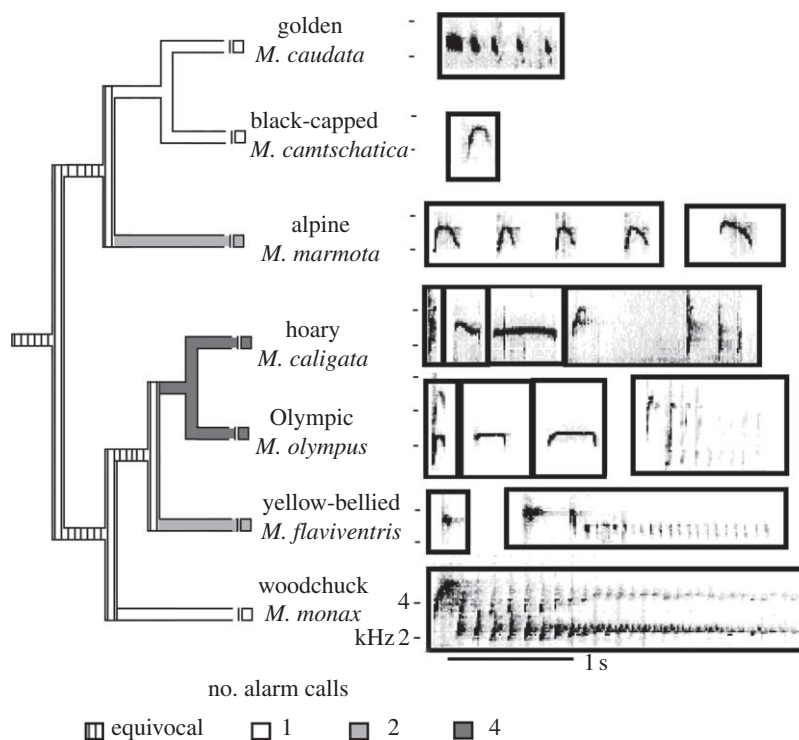


Figure 1. Alarm call repertoires of seven species of marmots (*Marmota* spp.). Sciurid rodents differ in the acoustic structure of their alarm calls and in the size of their alarm call repertoires.

variability of the signal's or system's parts, connections, or layers of meaning (table 1). For acoustic communication, attributes of communicative complexity can include a species' repertoire size (number of call types [32,39]) or the syntactical complexity or uncertainty [40,41] of sequences of calls. Signals may also be complex in their association with external referents, such as functionally referential alarm calls that communicate predator type or response strategy, in addition to alarm [42–45]. Communication of urgency or affective state is another form of complexity, providing additional information about the situation [46–48]. For example, many species of marmots alter the rate of their alarm calls with the urgency of the situation or the degree of risk [49]. The presence of embedded signature information (such as age, sex or individual caller identity [50–54]) also adds complexity to communicative signals.

As social complexity, however quantified, increases, more complex communication might be needed to manage this social complexity [55–59]. Attributes of social complexity may thus generate a need for animals to exhibit different types of communicative complexity.

2. SCIURIDS AS A MODEL SYSTEM

Sciurid rodents (Rodentia: Sciuridae), particularly ground-dwelling social species (tribe Marmotini, including ground squirrels *Spermophilus* spp. and related genera, prairie dogs *Cynomys* spp., and marmots *Marmota* spp.), present an excellent model comparative system for studying the relationship between social and communicative complexity, for several reasons.

First, ground-dwelling sciurids constitute a speciose clade that exhibits a wide range of social structures. On one end of the spectrum, some species are nearly solitary or live in simple family groups (e.g.

woodchucks, *Marmota monax*, live in groups of a mother plus her young of the year). Within the same clade, more complicated group structures are seen, such as those in Eurasian marmots (e.g. *M. caudata*, *M. marmota* [60]) in which young delay dispersal for one, two or more years, adult males participate in group life, and females may aggregate in harems or matriline. Social group size also varies considerably across ground-dwelling sciurids, as does group cohesion. In addition, sciurids also vary in their tiers or levels of social complexity [61,62], with some species exhibiting complex relationships between segregated social groups (e.g. some prairie dogs). Importantly, variation in social group size is not strictly tied to variation in other attributes of social structure [9], allowing these different attributes to be teased apart in comparative study.

Secondly, ground-dwelling sciurids offer a communication system amenable to comparative study. Ground-dwelling sciurids produce vocal alarm calls in response to predatory stimuli [63]. These calls are typically loud and perceptually salient, and they can be elicited and recorded by researchers. Within the sciurid alarm call system, an array of communicative complexity is exhibited. Species vary in the acoustic structure of their calls [39,54,64], the size of their alarm call repertoires [39,49] (figure 1), the response urgency or distance to predator encoded in their calls [65–67], syntactic or ordering differences in calls [64], and the degree to which age and sex and individual identity are encoded [54,68]. As with social complexity, we can view these as attributes of communicative complexity and they can be independently studied in comparative analyses.

Thirdly, published phylogenies [69–71] aid phylogenetically controlled evolutionary analyses in this taxon.

To date, two phylogenetically controlled studies have examined the correlated evolution of social complexity and communicative complexity in ground-dwelling sciurid rodents [39,54]. Importantly, comparative studies in sciurids permit us to decouple drivers of complexity, and, as discussed below, have revealed that social complexity, broadly defined, does not simply select for more complex communication. Rather, different attributes of sociality seemingly select for specific attributes of communicative complexity.

3. DEMOGRAPHIC COMPLEXITY DRIVES REPERTOIRE SIZE EVOLUTION

Blumstein & Armitage [39] used 22 species of ground-dwelling sciurids to test for a relationship between one attribute of social complexity (demographic role complexity) and one attribute of communicative complexity (alarm call repertoire size). They defined a social complexity index via information theory, using data on dispersal patterns, the age/sex composition of groups and variability in these traits [39]. The resulting numbers, expressed in bits, quantify the amount of information needed to describe the demographic role complexity in different species.

For species with multiple alarm call types, different call types may be used to communicate about different types of predators [42,43,45], to communicate different degrees of risk or response urgency [46,48], or to communicate both predator type and urgency [44,72]. Species living in more complex social groups, such as groups with more social demographic roles, may have greater need to signal alarm in a more complex manner and thus may use larger alarm call repertoires. Across ground-dwelling sciurids, alarm call repertoire size varies from one to five (see examples in figure 1). Blumstein & Armitage [39] used a combination of field recordings and literature review to establish the alarm call repertoire size for 22 species of sciurid and regressed this against the social complexity index. Demographic role complexity significantly explained variation in alarm call repertoire size, both in analyses of raw data and independent contrasts (figure 2).

More up-to-date phylogenies have since been published, so we re-ran the independent contrasts analysis using more recent phylogeny taken from Herron *et al.* [70] and Steppan *et al.* [71]. The relationship between social demographic complexity and alarm call repertoire size remained significant ($r^2 = 0.228$, $y = 1.049x$, $p = 0.025$, $n = 21$ independent contrasts). An increase in social demographic roles appears to drive the ability to communicate via a larger, more complex repertoire of alarm calls. The functional explanation underlying this correlation is unknown. Future study of alarm call type use in different contexts or between different caller–receiver dyads may be necessary to untangle how more demographically complex species may benefit from a more diverse alarm call repertoire.

4. SOCIAL GROUP SIZE DRIVES THE EVOLUTION OF INDIVIDUAL SIGNATURES

Pollard & Blumstein [54] compared sciurid vocal signature individuality (individual distinctiveness) against

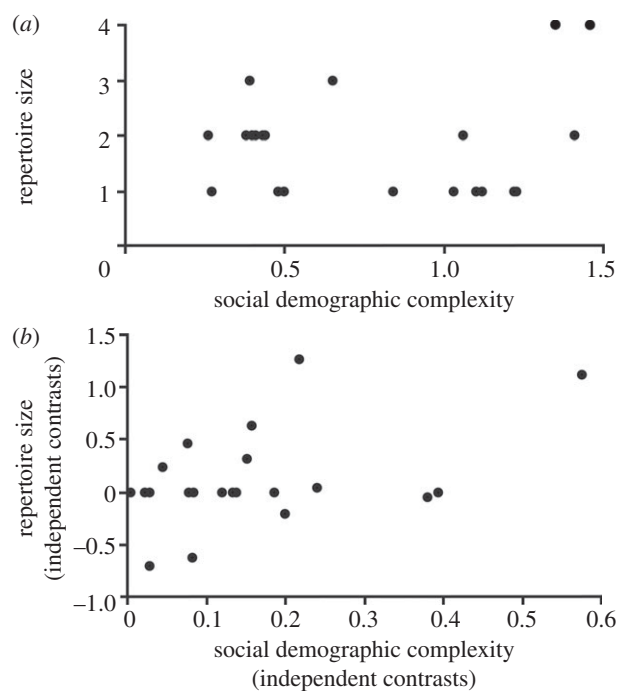


Figure 2. Relationship between social demographic complexity and alarm call repertoire size across 22 species of sciurid rodents, in raw (a) and independent contrasts (b) data. Social complexity (variability in demographic roles) correlates with alarm call repertoire size. (a) Adapted from Blumstein & Armitage [39], with permission from Chicago Journals.

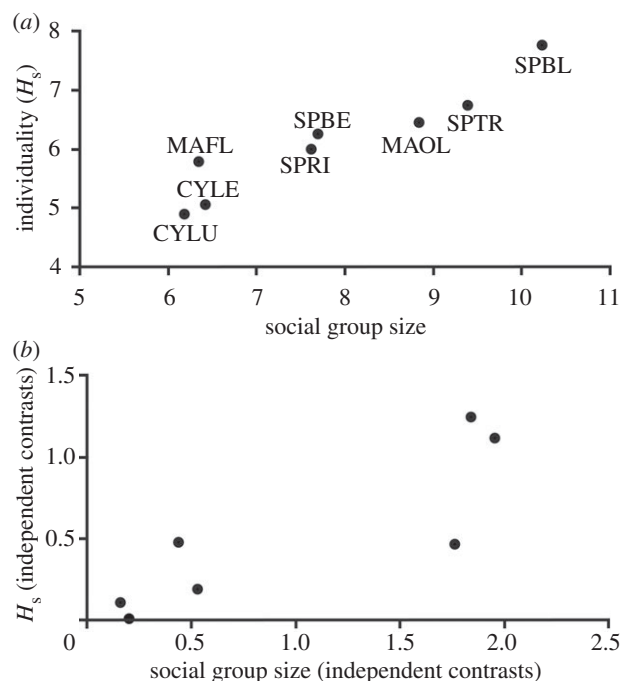


Figure 3. Relationship between social group size and alarm call individuality across eight species of sciurid rodents. In raw (a) and independent contrasts (b) data, social group size correlates with vocal individuality (H_s) in sciurid alarm calls ($r^2 > 0.88$, $p < 0.001$ in both cases). Species in (a) are *Cynomys leucurus* (CYLU), *C. ludovicianus* (CYLE), *Marmota flaviventris* (MAFL), *M. olympus* (MAOL), *Spermophilus beecheyi* (SPBE), *S. beldingi* (SPBL), *S. richardsonii* (SPRI) and *S. tridecemlineatus* (SPTR). Figure adapted from Pollard & Blumstein [54], with permission from Elsevier.

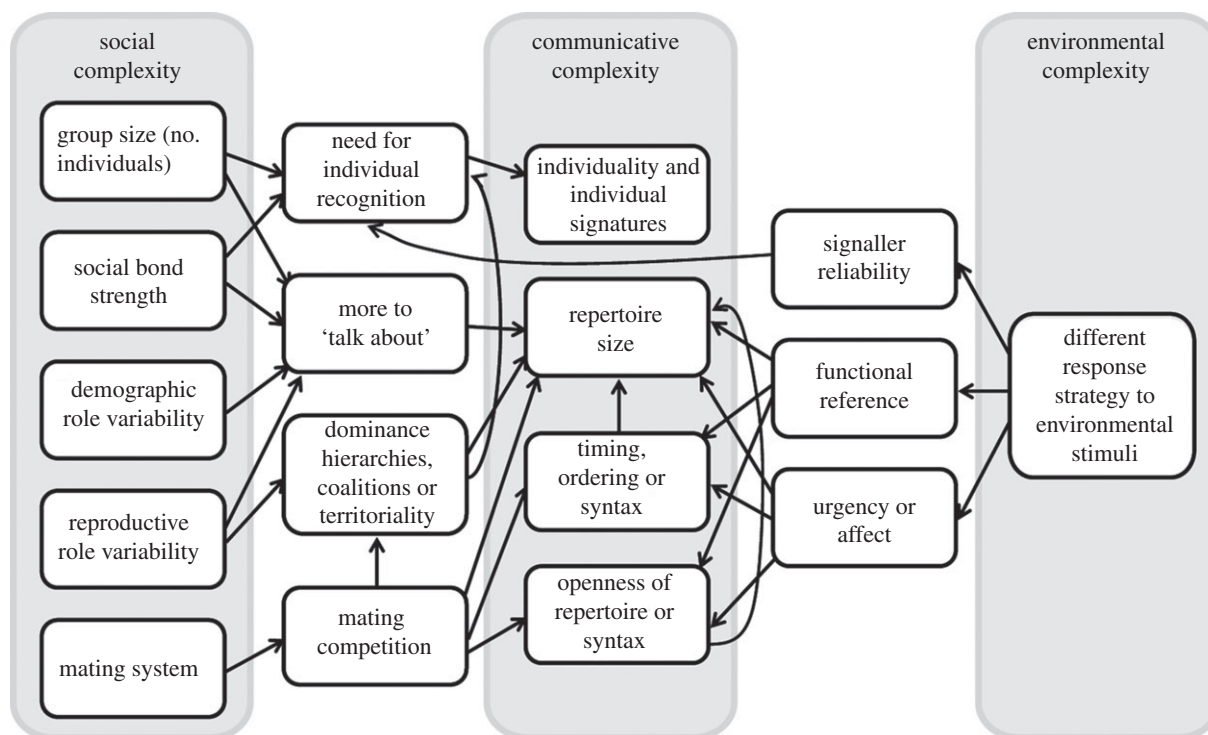


Figure 4. Possible functional relationships between attributes of social complexity and attributes of communicative complexity. For specific examples of relationships that are supported in the literature, see table 2.

social group size, Blumstein & Armitage's [39] demographic complexity index, and two other indices of social structure complexity [61,62]. Group size was not correlated with these other complexity indices [54]. Because studies quantifying vocal individuality are not common, this analysis required novel data, and eight species of ground-dwelling sciurid were thus captured, individually marked and recorded on multiple occasions. Individuality was calculated from acoustic traits using an information-theory metric developed by Beecher [5,73] and used in previous studies [25,27,52,74]. The individuality information statistic quantifies, in bits, the amount of individually specific information content present in a species' vocalizations. This statistic was used as the quantitative metric of one attribute of communicative complexity.

Individual signatures in alarm calls are important for animals such as sciurids [75–77]. Individuals vary in their alarm signal reliability, and listeners benefit when they recognize the individual identity of an alarm caller, as this allows them to better calibrate their behavioural response [76–80]. Ground-dwelling sciurids live in groups of closely related kin, such that the signaller and receiver are often close relatives. This may allow callers to benefit via kin selection by aiding related receivers in individual discrimination and reliability assessment [54,77], although they may also benefit via reciprocal altruism [81].

Individuality is expected to evolve with group size [5,25–27,52,54,73]. As social group size increases, the number of individuals that must be discriminated increases accordingly, making individual recognition tasks more difficult. Increased individuality would be necessary to permit successful discrimination of all the individuals in the group. Since other attributes of

sociality affect communicative complexity [39,82], these other attributes may also influence individuality.

Pollard & Blumstein [54] gathered typical social group size data from the literature and regressed this against the individuality metric. Group size explained considerable variation in vocal individuality, both in the raw data and in an analysis using independent contrasts (figure 3). As predicted, social group size appears to drive the evolution of individual signature information.

Interestingly, it is group size, not other social complexity attributes, that seems responsible for the evolution of individually specific vocalizations. Signature information was also regressed against three other measures of social structure complexity, including Blumstein & Armitage's [39] demographic complexity index, Michener's [62] social grade, and Armitage's [61] sociality index. 'Social grade' and 'sociality index' are somewhat subjective numerical assignments intended to quantify the complexity of each species' social structure and mating system. Individuality was not significantly related to any of these three other social complexity attributes, even after controlling for variation in group size.

5. ATTRIBUTES OF SOCIALITY, ATTRIBUTES OF COMMUNICATION

Results from sciurid studies highlight an important caveat about the evolution of social and communicative complexity. Both sociality and communication have multiple attributes (table 1), and these attributes affect one another in complex ways (figure 4). The main insight from our integrative overview is that different attributes of social complexity are likely to drive different attributes of communicative complexity. Thus, it is

Table 2. Comparative relationships among attributes of social and communicative complexity. Studies indicate that different attributes of social complexity affect different attributes of communicative complexity.

attribute of social complexity	attribute of communicative complexity	taxon	no. species in study	signal type	phylogenetic control	citation	details
social group size	potential for repertoire size	anthropoid primates	12	facial expressions (visual)	generalized	[35]	social group size predicts facio-muscular ability to produce varied facial expressions
social group size	repertoire size	primates	42	vocalizations (auditory)	least-squares independent contrasts	[32]	social group size predicts repertoire size for adult vocalizations
social group size	signal variability	whales	34	vocalizations (auditory)	independent contrasts	[83]	social group size predicts the amount of tonal modulation in cetacean whistles
social group size	potential to perceive diverse repertoire	strepsirrhine primates	11	acoustic signals (auditory)	none	[84,85]	foraging group size predicts auditory sensitivity and high frequency hearing
social group size	individuality	sciurid rodents	8	vocal alarm calls (auditory)	independent contrasts	[54]	social group size predicts individual distinctiveness in vocal alarm calls
colony size	individuality	<i>Hirundo</i> swallows	2	vocal contact calls (auditory)	comparison within genus	[25]	nesting colony size predicts individual distinctiveness in chick begging calls
colony size	individuality	<i>Larus</i> gulls	2	vocal contact calls (auditory)	comparison within genus	[26]	mobile crèche size predicts individual distinctiveness in adult 'long calls'
colony size	individuality	microchiropteran bats	8	vocal contact calls (auditory)	none	[27]	roosting colony size predicts individual distinctiveness in infant isolation calls
diversity/variability of demographic roles	repertoire size	sciurid rodents	22	vocal alarm calls (auditory)	independent contrasts	[39]	diversity/flexibility in demographic roles within social groups predicts repertoire size for vocal alarm calls
diversity/variability of reproductive roles	individuality	<i>Polistes</i> wasps	25	facial coloration patterns (visual)	concentrated changes	[82]	flexibility in nest-founding strategies predicts variability (individual distinctiveness) in visual facial markings
social structure complexity	repertoire size	<i>Eulemur</i> lemurs	8	glandular chemical secretions (olfactory)	none	[86]	social structure predicts diversity of odour chemicals in female perianal secretions
social structure complexity	repertoire size	<i>Papio</i> and <i>Theropithecus</i> monkeys	2	acoustic signals (auditory)	none	[87]	social structure predicts vocal repertoire size
mating system complexity	repertoire size	phocid seals	12	underwater vocalizations (auditory)	none	[88]	mating system predicts repertoire size for male underwater vocalizations
mating system complexity	repertoire size	lizards	41	bodily ornamentation (visual)	model fitting	[89]	mating system predicts the number of bodily ornaments and colour dichromatism
social bonding	repertoire size	primates	20	vocalizations (auditory)	independent contrasts	[32]	time spent in social grooming predicts repertoire size for adult vocalizations
social bonding	potential for repertoire size	catarrhine primates	10	facial expressions (visual)	generalized least-squares	[90]	time spent in social grooming predicts facial nucleus volume in the brain

important to think clearly about the nature of the relationship because different attributes work different ways (see also [1]). Studies from other taxa also support taking a nuanced look at the correlated evolution of social and communicative complexity (table 2). For example, the complexity of reproductive roles was found to influence individuality in wasp facial markings [82], while nesting or roosting colony size was found to influence individuality in avian and chiropteran contact calls [25–27]. In phocid seals, underwater repertoire size increased with mating system complexity [88]. In primates, social group size and time spent in social grooming influenced vocalization repertoire size [32], while group size influenced ability to produce varied facial expressions [35]. Furthermore, social complexity may influence not just the complexity of communicative signals themselves but also the perceptual capacity to receive such signals, e.g. social group size predicts auditory sensitivity in lemurs [84]. Social and communicative complexity can also covary within species or on short time scales; for example, chickadees placed in larger groups displayed more variability in their call types and combinations [40]. In all these cases, a different attribute of social complexity is associated with a different attribute of communicative complexity.

As a general rule, we would predict that the types of communicative complexity that are most relevant to a specific aspect of sociality would be evolving with those aspects of sociality. For example, if individual recognition is important, and if all members of a group must be recognized, we would predict a specific type of communicative complexity (individualistic signatures) to evolve with a particular attribute of social complexity (group size). This has been found in birds, bats and sciurids [25–27,54]. If calls are used to attract or impress mates, we would predict specific attributes of communicative complexity (such as syntactical complexity or repertoire size) to evolve with a specific attribute of social complexity (mating system). Indeed, male repertoire size seems to have evolved with mating system in phocid seals [88]. However, these relationships are not always obvious, and attributes of sociality may influence communication in diverse and complicated ways (figure 4). Future studies in more taxa will be necessary to comprehensively identify the many ways in which distinct attributes of social and communicative complexity are evolutionarily or functionally linked. With the discovery that social network statistics can be used by behavioural biologists [18,91,92], there are many precisely defined attributes of sociality that could be studied. From a comparative perspective, available data are often a limiting factor, but over time, there will be more data from different species available with which to study the evolution of social and communicative attributes [93]. As these databases are developed, sciurid rodents can continue to play a valuable role in this pursuit, because these species vary in several attributes of social and communicative complexity, and systematic study can help identify which of these attributes covary. These attributes can be further examined with respect to different environmental conditions in sciurids' diverse habitats, and/or mapped onto available phylogenies to estimate when and how complexity evolved.

6. CONCLUSIONS

The relationship between social complexity and communicative complexity is multi-faceted. Different attributes of sociality may drive the evolution of different attributes of communication. For example, in sciurid rodents, social demographic complexity explains the evolution of alarm call repertoire size, while social group size explains the evolution of alarm call vocal individuality. Sciurids are one of many excellent model systems in which to explore the evolution of social and communicative complexity, and future work in sciurid and non-sciurid taxa will help build a comparative database in which these questions can be thoroughly examined. The ever-growing comparative database will ultimately help us develop a comprehensive understanding of how social complexity and communicative complexity evolve.

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