REVIEW

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A framework for studying social complexity

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Abstract

Social complexity has been one of the recent emerging topics in the study of animal and human societies, but the concept remains both poorly defined and understood. In this paper, I critically review definitions and studies of social complexity in invertebrate and vertebrate societies, arguing that the concept is being used inconsistently in studies of vertebrate sociality. Group size and cohesion define one cornerstone of social complexity, but the nature and patterning of social interactions contribute more to interspecific variation in social complexity in species with individual recognition and repeated interactions. Humans provide the only example where many other unique criteria are used, and they are the only species for which intraspecific variation in social complexity has been studied in detail. While there is agreement that complex patterns emerge at the group level as a result of simple interactions and as a result of cognitive abilities, there is consensus neither on their relative importance nor on the role of specific cognitive abilities in different lineages. Moreover, aspects of reproduction and parental care have also been invoked to characterize levels of social complexity, so that no single comprehensive measure is readily available. Because even fundamental components of social complexity are difficult to compare across studies and species because of inconsistent definitions and operationalization of key social traits, I define and characterize social organization, social structure, mating system, and care system as distinct components of a social system. Based on this framework, I outline how different aspects of the evolution of social complexity are being studied and suggest questions for future research.

Significance statement

Animal and human societies differ in social complexity, i.e., the number and association patterns of group members as well as the nature and patterning of their social relationships, but the dimensions of social complexity, the processes that generate it, the selective forces that engender different levels of social complexity, and the evolutionary consequences of this variation remain to be comprehensively understood. Here, I offer a conceptual framework for the systematic and comparative studies of social complexity by defining its main components as well as their proximate and ultimate relationships.

Keywords Social complexity · Animal societies · Social organization · Social structure · Behavior · Evolution

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Introduction

The systematic comparative study of animal societies over the last century (Espinas 1878; Deegener 1918; Allee 1927; Wheeler 1928; Scott 1956; Crook 1970; Wilson 1971, 1975; Smuts et al. 1987; Lee 1994; Clutton-Brock 2016; see also Rubenstein and Abbot 2017a) has revealed stunning interspecific diversity in the size, composition, and cohesion of social units, as well as in the patterning of reproductive skew, cooperation, and competition among their members. This diversity has historically been perceived as reflecting a natural gradient that has been expressed as either categorical or continuous variation in social complexity (see below and Dew et al. 2016; Rubenstein et al. 2016). Even though understanding

the causes and consequences of variation in social complexity is central to understanding the diversity and evolution of animal societies, social complexity remains both poorly characterized and incompletely understood, however, and it has therefore been recently identified as one of the remaining frontiers in the study of animal behavior (Bradbury and Vehrencamp 2014).

In this paper, I argue that inconsistent definitions of the features of social systems contributing to social complexity, a lack of relevant operational definitions applicable to a wide range of species, variation in conceptual and methodological approaches used in the study of social insect and vertebrate societies, and lack of a general consensus on its key determinants and consequences have hampered progress towards a better understanding of social complexity. Therefore, I offer a conceptual framework for the systematic and comparative study of social complexity by defining its main components as well as their proximate and ultimate relationships.

Patterns of social complexity and their underlying processes

Anyone staring at a busy ant colony, witnessing the versatile flight maneuvers of a flock of starlings or observing the manifold interactions among the members of a primate group, must be impressed by the level of behavioral complexity exhibited by these and many other animal species. It is therefore not surprising that the current literature on the study of animal societies has increasingly included reference to their social complexity. However, researchers studying different taxa have been using different criteria and technical terms to define levels of social complexity (Rubenstein and Abbot 2017b), with a pronounced divide between studies of invertebrate and vertebrate societies (Rubenstein and Abbot 2017a).

Presumably, going back to the notion of a natural progression of societies from simple to more complex ones first proposed by Spencer (1895), classification of the social systems of social insects has always invoked a gradient of increasing social complexity (Wheeler 1910, 1928) based on the presence/absence of three key features. Species with overlapping generations, cooperative brood care, and reproductive division of labor, which not only are widespread among hymenoptera and termites but also found in beetles, aphids, thrips, and shrimp, have been defined as "eusocial" (Batra 1966) and are widely considered to represent the highest level of sociality or social complexity. Species exhibiting various combinations of permutations of only one or two of these traits have been classified as solitary, subsocial, communal, quasi-, or semisocial, respectively (Michener 1969; Wilson 1971; Crespi and Yanega 1995; reviewed in Dew et al. 2016; see also Costa and Fitzgerald 2005) and therefore as representing less socially complex or somehow less social

forms. This terminology continues to be widely used by students of invertebrate societies, and it has recently been refined by recognizing the existence of casteless species, i.e., those without lifetime commitment to queen-like or worker-like roles despite the existence of skew in reproduction or alloparental care (Dew et al. 2016).

Among vertebrates, some obligate cooperative breeders, which share the three defining traits with eusocial invertebrates (Sherman et al. 1995), have also been depicted as "highly social" (e.g., Bateman et al. 2012) or as representing "the highest level of social complexity" (e.g., Fischer et al. 2017a), but it remains unclear whether the presence or absence of cooperative breeding represents the only or only one important criterion for this assessment. As a result, the distinction among cooperative breeding, eusociality, and social complexity has always been somewhat blurred. While one can see why some authors studying vertebrates also emphasize cooperative breeding as a key criterion for assessing the degree of social complexity to highlight similarities with social insects, different non-cooperative breeders have also been characterized as "highly social" (e.g., Kelly and Goodson 2015; Markham et al. 2015; Reisinger et al. 2017), often without an explanation for this classification. Only "communal breeding," as originally defined for invertebrates (Michener 1969), has been consistently used to classify vertebrate societies (with respect to the number of co-breeding females: Brown 1978; Doody et al. 2009; Clutton-Brock 2016). Last but not least, vertebrate social complexity has often been operationalized as variation in group size (e.g., Dunbar and Shultz 2007; Freeberg et al. 2012), whereas group size variation has played a smaller role in studying insect social complexity (but see, e.g., Bourke 1999; Ferguson-Gow et al. 2014; Feinerman and Traniello 2016).

We therefore lack both a general concept of which features of a social system contribute to social complexity, whether and how they can be ranked in any meaningful way, and whether a single framework can accommodate studies of both invertebrates and vertebrates. Additional interesting questions in this context address the processes, correlates, consequences, and evolution of social complexity. I will address each of these aspects below after outlining a general concept of social complexity.

Defining social complexity

Very generally speaking, complexity is the opposite of simplicity. A system is said to be complex if its parts are neither arranged completely randomly nor completely ordered. According to a very general definition, which also applies to phenomena in physics or molecular biology, for example, "complex systems are made up of multiple parts that interact in multiple ways, generating non-linear emergent effects that are greater than the sum of its parts" (wikipedia.org). These aspects are also evident in a recent definition of social

complexity: "Complex social systems are those in which individuals frequently interact in many different contexts with many different individuals, and often repeatedly interact with many of the same individuals over time" (Freeberg et al. 2012). Thus, the number of individuals and their interactions represent two key components of social complexity, so that a pair-living species with virtually no social interactions represents a baseline of social complexity (Dröscher and Kappeler 2013).

Because species in which adult individuals lead solitary lives are typically not in the focus of studies of social complexity, the "number of individuals aspect" usually refers to the size of groups or other social units. Variation in group size is a key determinant of social complexity because it can affect group cohesion, group composition (especially the adult sex ratio), association patterns, and reproductive skew, all of which arguably contribute to social complexity. Specifically, with increasing group size, there is more potential for a decrease in spatio-temporal cohesion, and thus an increasing potential for fission-fusion dynamics (Aureli et al. 2008; Couzin and Laidre 2009), because more individuals have more options for distributing themselves in space and time. Moreover, larger groups also have a greater potential for multi-level structuring, i.e., the presence of multiple functional subunits (Grueter et al. 2012) and patterns of spatial assortment (Farine et al. 2017), whereas the potential for larger changes in the adult sex ratio decreases with increasing group size (Kappeler 2017). Furthermore, larger groups in eusocial species are characterized by a reduction in workers' reproductive potential, the degree of caste determination, and the intensity of reproductive conflict (Bourke 1999).

In terms of processes contributing to social complexity, there is much interspecific variation in whether individuals form groups or not, in the optimal size of groups, in how stable and permanent groups are in space and time, in whether social units contain members of different generations, in whether males and females are permanently associated, and in the adult sex ratio of group members. Intraspecific variation in these traits has remained understudied even though Lott (1991) highlighted its prevalence and significance decades ago. The various ultimate costs and benefits modulating corresponding variation among species have been relatively well studied by behavioral ecologists (Pulliam and Caraco 1984; van Schaik and Kappeler 1997; Conradt and Roper 2000; Krause and Ruxton 2002; Székely et al. 2014), however, and the proximate behavioral mechanisms generating this variation are largely studied as demographic and life history variables, such as births, deaths, maturation, and dispersal events (Greenwood 1980; Geffen et al. 1996; Ancona et al. 2017).

Even though quantity can have a quality all its own, it has long been recognized that the nature and patterning of social interactions contributes a qualitative component to social complexity that is independent of the emergent properties due to variation in group size alone (Dunbar and Shultz 2010). However, the complexity of social interactions is not completely independent of group size because the number of individuals an animal can interact with increases linearly with group size and because the number of all potential dyads among group members increases exponentially with group size. When the same individuals interact repeatedly, the emergent properties of these repeated interactions can be described as social relationships (Hinde 1976), which, in turn, can differ in at least seven dimensions (frequency, diversity, symmetry, tenor, tension, predictability, and stability; Silk et al. 2013). Social complexity is also enhanced by interactions that involve more than two individuals simultaneously, creating, for example, opportunities for audience effects (Zuberbühler 2008), eavesdropping (Valone 2007) and coalitionary intervention (Harcourt and de Waal 1992).

Social interactions and relationships contribute to more social complexity when interactions take multiple forms and occur in different contexts, when individuals recognize each other, memorize past interactions, have many opportunities to interact with the same individuals again in the future, and if they modify their behavior in response to previous interactions (de Waal and Tyack 2003). Variation in these aspects of social interactions depends foremost on the type of group, i.e., whether they are transient aggregations or permanent societies, as well as on lineage-specific life history traits, especially longevity. These factors broadly explain, for example, why dolphins and ravens have richer and more diverse social interactions than herring or termites. Importantly, the patterning and nature of social interactions are functionally relevant because fitness of individuals in group-living species depends in part on the outcome of their interactions with other group members (Silk 2012), which is highly unpredictable because conspecifics differ in multiple internal and external states as well as in their social competence (Taborsky and Oliveira 2012). Thus, variation not only in group size but also in behavioral traits contributing to social complexity has fitness consequences.

Whereas there is a broad consensus about the contribution of social interactions and relationships to social complexity, there is some controversy about the relative importance of processes of self-organization in this context. This discussion has two components. One is concerned with the question whether and to what extent processes of self-organization contribute to observed patterns of complexity in social structure. Self-organization is now recognized as an important determinant of highly structured collective behavior not only in social insects (Bonabeau et al. 1997; Fewell 2015) but also in vertebrates on the move (Couzin and Krause 2003; Farine et al. 2017), foraging behavior (Farine et al. 2014; He et al. 2019), dominance hierarchies, and other differentiated relationships (Hemelrijk et al. 2008, 2017; Franz et al. 2015). Thus, simple

behaviors at the individual or dyadic level can give rise to complex patterns at the group level.

The more controversial component has to do with the putative required cognitive underpinnings. The rich diversity of complex social relationships, particularly in primates and other mammals, has been attributed to, or at least associated with, enhanced brain size and special cognitive abilities, such as the attribution of mental states to others (Seyfarth and Cheney 2015), according to some authors (e.g., de Waal and Tyack 2003; Sewall 2015; Platt et al. 2016), whereas others emphasize the fact that complex patterns can be reproduced with relatively simple models and, hence, without any special cognitive abilities (e.g., Barrett et al. 2007; Hemelrijk et al. 2017; Kershenbaum and Blumstein 2017). This apparent controversy might be resolved by more detailed and careful analysis of which specific behavior patterns require which specific cognitive abilities.

Quantifying social complexity

If it is interesting or meaningful for a specific question to compare levels of social complexity across species, we require a scale that ideally integrates measures of both group size and relationship diversity. Most previous studies have focused on either one of these measures, however. Blumstein and Armitage (1998) proposed an index of social complexity that integrated information on interspecific variation in the representation of different age and sex classes. This index therefore included more information than group size alone, but it did not account for social interactions. Avilés and Harwood (2012) proposed a continuous index of sociality based upon measures of philopatry, grouping tendencies, and the tendency of individuals to contribute to reproductive altruism. This index, however, is only applicable to cooperative breeders because of its third component, which requires intraspecific variation in sociality (proportion of nest or colonies consisting of solitary and multiple adult individuals). This sort of variation is rare or poorly documented in most animal lineages, and this index ignores sex differences in philopatry, which are common among vertebrates.

Other measures of social complexity focused on social relationships. Bergman and Beehner (2015) recommended that social complexity should be measured as the number of differentiated relationships that individuals have, where "differentiated relationships are those that can be distinguished by an observer." This proposal does not acknowledge variation in group size, however, and it may generate data that are difficult to compare across taxa because of the unspecific nature of the operational recommendation, however. Fischer et al. (2017b) proposed a more specific procedure to quantify the diversity of differentiated relationships among group members, but it did not incorporate information on group size either. Finally, social network analyses can generate a number of metrics based on a given number of individuals and a given type of behavioral variable (Krause et al. 2007; Farine and Whitehead 2015; Kurvers et al. 2014; Weiss et al. 2019), but in most studies, only one behavioral variable has been included at a time and, more importantly, the resulting network metrics cannot easily be compared between groups of the same species, let alone across species. Dynamic (Farine 2018) and multi-layer social networks (Boccaletti et al. 2014) may provide a promising future option for generating more comprehensive objective measures of social complexity, however. Thus, at the moment, there is no single comprehensive measure or index of animal social complexity that can be used for meaningful interspecific comparisons or rankings.

Humans provide an interesting exception in this context, however, because they exhibit massive intraspecific variation in social complexity that has additionally also changed over time. In the past, scholars in history, archeology, sociology, anthropology, and other related disciplines have used very different and mostly single measures of social complexity (population size: Marquet et al. 2012; Vaesen et al. 2016; group size: Derex et al. 2013; warfare: Turchin et al. 2013; connectedness of populations: Muthukrishna et al. 2013; age structure: Lienard 2016). A recent multi-disciplinary collaborative project that also included evolutionary biologists used a list of 51 variables that reflect the size and hierarchical complexity of social units along with some human-specific features, such as the information and monetary system (Turchin et al. 2018). Surprisingly, a single principal component captured 77% of the variance among more than 400 societies from 30 regions around the world, indicating not only interesting functional relationships among these variables, but also that it should be possible to develop reliable measures of social complexity for animal societies with similar procedures as well.

A century of "social'ism"

Given these practical difficulties with developing a comprehensive quantitative index of overall social complexity, a systematic qualitative inventory of social and life history variables may provide a basis for a meaningful ranking and for identifying key factors in different taxa. Most such existing comparisons focused on particular lineages (e.g., Wilson 1971; Smuts et al. 1987; Connor et al. 1998; de Waal and Tyack 2003; Wolff and Sherman 2007), which has the advantage of controlling for variation in fundamental life history traits. Thus, comparisons of levels or categories of social complexity among mammals or among carnivores might be both easier and more meaningful than comparisons across all vertebrates or animals. Only one recent research program offered a broad comparative perspective covering all main social lineages (Rubenstein and Abbot 2017c). Apart from many new insights about social evolution (Rubenstein and Abbot

2017b), this broad comparison also highlighted a key problem of comparative studies: inconsistent definitions and operationalization of key social traits across studies hamper both general and quantitative comparisons.

The arbitrary use of "social" in combination with various nouns lies at the heart of this problem. Social behavior, social structure, social organization, social system, social roles, social strategies, and several other similar terms have been and are being used to refer to both the same and very different aspects of sociality in different studies. In particular, the two main components of social complexity—group size and composition as well as patterns of social relationships—have both been referred to as social organization and social structure, making it impossible to infer from the title of a study alone which aspect was examined. Sometimes, these terms are even used synonymously in the same paper (see, e.g., Nandini et al. 2017 for a recent example) or to define each other (see, e.g., McFarland 2014). This rampant "social'ism" creates at least three fundamental problems.

First, in contrast to say physicists, neurobiologists, or immunologists, which study clearly defined nuclear particles, brain regions, or molecular processes, respectively, as students of social behavior, we jeopardize our scientific reputation in both the scientific community and the public at large because we can apparently not agree on even the most fundamental definitions of our study objects. Second, the lack of a generally agreed upon vocabulary also hampers conceptual progress within our own discipline, where various formal and verbal models (e.g., Nonacs and Hager 2011; Clutton-Brock and Janson 2012) have played important roles in guiding research, but different scholars use different terms for the same model components. Finally, a lack of consensus on how to label and define different features of a social system comes with the risk that variables with the same label (e.g., "monogamy") may contain different measures (in this example pair-living, pair-bonding, genetic monogamy and solitary breeding; Kappeler 2014; Tecot et al. 2016), leading to an enhanced risk for comparative studies to reach different conclusions even though they are based on the same primary studies (see, e.g., Lukas and Clutton-Brock 2013; Opie et al. 2013). I therefore think that there is an urgent need to agree upon commonly used definitions in the study of animal sociality. As in taxonomy, where different names were often proposed for the same species by different authors, the principle of priority should also provide objective guidance on the proper use of existing synonyms in the study of animal sociality.

So, who introduced and defined the key terms characterizing a social system? The first comparative discussion and classification of animal societies were conducted by Alfred Espinas (1878), who distinguished between "accidental" and "normal" societies, of which he recognized two types (primitive and advanced), and contrasted both of these with groups ("peuplades"), which are, according to him, held together by kin ties and reproduction. Espinas not only had a surprisingly profound modern understanding of animal societies given the available information at the time, but he also distinguished between temporary and permanent groups, and, in discussing interspecific variation in their size and composition, consistently used the term "organization" (e.g., on p. 491). He also noted variation among societies in their "complexité organique" and considered the social organization of mammals to be "a little bit higher." Paul Deegener (1918) also emphasized the difference between "accidental" and "essential" societies, but his complete classification scheme proposed 92 categories of social organization (he only used the term "Gesellschaften," i.e., "societies") expressed in unwieldy Greek terminology.

In the twentieth century, Wheeler (1910) provided the first comprehensive description of the "social habit" of ants and other insects, a term adopted by Allee (1927), who also discussed the evolutionary origins of "more advanced forms of social life." Allee was mainly concerned with group size and composition and compared levels of complexity ("the highest type of social organization, such as occurs in ants and termites, …."), but he also used "social structure" to refer to the same traits, in both cases without defining either term. In a later paper, Allee (1942) discussed data on dominance in birds and mice and used "group organization," "social organization," and social structure to refer to the observed hierarchies. Similarly, Scott (1956) referred to the description of basic patterns of social behavior and their organization into social relationships as the study of social organization. Influential early papers in behavioral ecology (e.g., Crook 1970) also used social structure and social organization to refer to group size and composition as well as to interindividual relations. It was not until Peter Jarman (1974) consistently referred to group size and composition as social organization, and Robert Hinde (1976) provided a clear definition of social structure, which he used consistently to refer to the emergent patterning of dyadic social relationships, that social terminology was used more carefully, however.

The components of social systems

Based on the historical precedency of key terms discussed above, I advocate the consistent use of the following terms to describe and study the components of the *Social system* of a species (see Fig. 1 and also Kappeler and Schaik 2002). *Social organization* refers to the size and composition of a social unit. These are two demographic features that can simply be determined (assuming different age/sex classes are easily distinguishable) without knowing or assuming anything about how these individuals interact with each other. In describing patterns of social organization, it is necessary to identify these species-specific social units, such as solitary individuals, pairs, aggregations, colonies, groups, or societies. A fundamental distinction
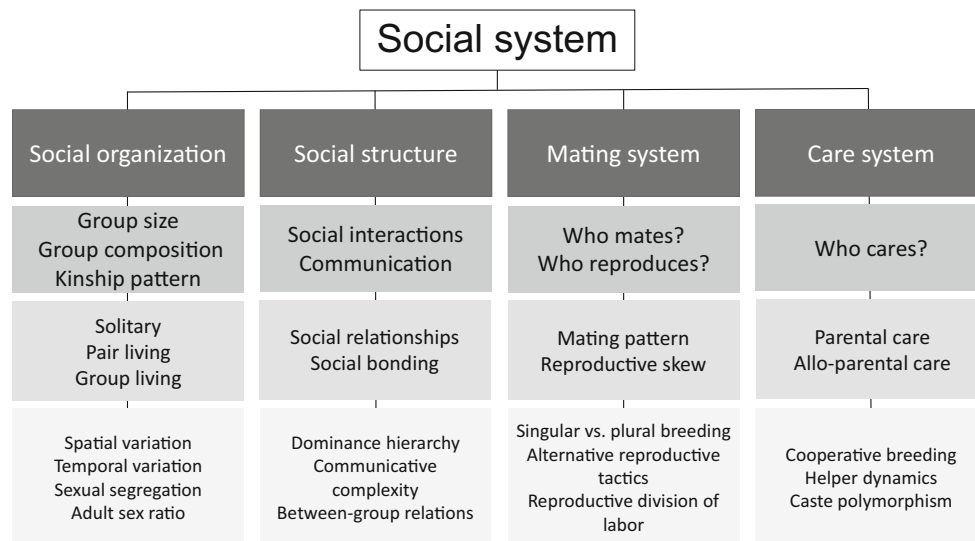
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Social organization	Social structure	Mating system	Care system
Group size Group composition Kinship pattern	Social interactions Communication	Who mates? Who reproduces?	Who cares?
Solitary Pair living Group living	Social relationships Social bonding	Mating pattern Reproductive skew	Parental care Allo-parental care
Spatial variation Temporal variation Sexual segregation Adult sex ratio	Dominance hierarchy Communicative complexity Between-group relations	Singular vs. plural breeding Alternative reproductive tactics Reproductive division of labor	Cooperative breeding Helper dynamics Caste polymorphism

Fig. 1 A framework for the study of social systems and social complexity. The first row indicates the four core components of a social system. The second row lists the main variables or questions addressed by each component. The third row contains key features of a social system that provide a general characterization of a given species. The bottom row lists more specific aspects that contribute to social complexity. The differentiation between rows 2 and 3 is somewhat arbitrary, whereas the separation into different columns is not. See text for detailed explanation

exists between solitary individuals and those that spend the majority of their activity period in association with at least one other adult conspecific. Non-solitary social units can be operationally defined as "a set of animals that interact regularly and more so with each other than with members of other such groups" (Struhsaker 1969), where interaction in this context should refer to association. Variation in spatial cohesion or temporal persistence may make this task operationally challenging in some taxa, however (e.g., Whitehead 2008; Schneider and Kappeler 2016). The smallest group size equals 2; the largest animal groups can include millions of individuals (Parrish and Edelstein-Keshet 1999). Group composition will typically refer to the sex and age of group members, which are also often strong predictors of kin relations. Additional aspects of the genetic structure of a social unit can be inferred from behavioral data (who disperses? Which sex is philopatric?), whereas more fine-grained description of kinship patterns requires genetic analyses.

Social structure is defined by the content, quality, and patterning of social relationships emerging from repeated interactions between pairs of individuals belonging to the same social unit. In species where individuals interact little, often in very similar forms and in the same contexts, it is not possible to identify differentiated relationships because these species also typically lack individual recognition. Social bonds represent a subset of differentiated relationships with particular characteristics (high affiliation and low agonism) and often have functional importance (Silk 2012; Silk et al. 2013; Seyfarth and Cheney 2015). Dominance relationships develop as a result of repeated agonistic interactions and represent a functionally important aspect of social structure because they regulate access to resources and mates in many species. In some species, dominance relationships may be established or stabilized by polyadic interactions, such as

coalitions or redirected aggression, and agonistic interactions can be followed by post-conflict interactions, such as reconciliation or consolation, that enhance social complexity (Aureli et al. 2012). Because acts of intraspecific communication also represent forms of social interaction, I consider communicative complexity to constitute a core aspect of social structure (see also Wilson 1971), rather than a separate entity being driven by social complexity (see below). An often neglected aspect of social structure concerns relationships between neighboring social units, which can vary massively in mutual tolerance (Willems and van Schaik 2015). Matings and other sexual interactions are excluded from the set of social interactions as they define a distinct functional component of the social system. Social network analyses and other methods provide modern quantitative measures of different dimensions of social structure, including their temporal dynamics (Krause et al. 2007; Neumann et al. 2011; Farine 2018) and the relative importance of direct and indirect social relationships (Brent 2015).

Because mating interactions have direct fitness consequences, and because there is no 1:1 relation between social organization and mating patterns (Kappeler and Schaik 2002; Rubenstein and Abbot 2017a), the *Mating system* represents a distinct component of every social system. Studies of mating systems can yield information on the identity and average number of mates of males and females. These data based on behavioral observations can be complemented with genetic data to reveal who actually reproduced (i.e., who fertilized the eggs). The resulting emergent patterns at the level of the social unit allow classification of species as monogamous, polygynous, polyandrous, or polygynandrous (i.e., promiscuous), adjectives that should not be used to refer to types of social organization to acknowledge their conceptual

separation. For most species, it will be easy to determine whether a single or multiple females breed and/or whether there is a reproductive division of labor. However, interindividual variation in mating and reproductive success often require more detailed studies to determine patterns of male and female reproductive skew, Bateman gradients or the existence of alternative reproductive tactics.

Finally, because the categories of social systems defined by specialists studying different taxa regularly also include aspects of parental care (Rubenstein and Abbot 2017b), I propose the *Care system* as the fourth component of a social system. By detailing who cares for dependent young, information on either the absence of parental care or on maternal, paternal, bi-parental, or allo-parental care can be provided. This component will also specify the presence of cooperative breeding as well as caste polymorphism in species where they play a role. Together, these four components define the cornerstones of a social system and provide a basis for the systematic study of social complexity.

A final comment on practical difficulties with studying any or all components of a social system is indicated. These difficulties arise from the fact that any empirical study including several social units is bound to find variation among them. Thus, a key problem for making general statements about "the social system of species x" as well as for extracting data from primary studies for quantitative comparative studies is how to deal with intraspecific variation (see, e.g., Lukas and Clutton-Brock 2017; Schradin 2017). This variation exists among neighboring social units, within social units over time, and sometimes among different populations of a given species. In cases where such variation is measured on a continuous scale, such as group size or grooming rates, the appropriate descriptive statistic such as the median or the (weighted) mean can be reported and used, respectively. Repeated measures of the same social units over time, which are increasingly available from long-term studies, require a justified criterion for non-independence so that data on group size, adult sex ratio, or the number of helpers, for example, can be used for determining the appropriate central tendencies. It will largely depend on the species' life history whether such repeated measures will be statistically independent after a week, month, year, or even longer periods.

In cases where intraspecific variation occurs on a categorical scale, classification can be more challenging. In classifying a species as either group or pair living, for example, species that switch between these two states from year to year (e.g., striped mice: Schradin 2013), have adjacent groups with either social organization (callitrichids: Garber et al. 2016), or exhibit other patterns of intraspecific variation (Lott 1991) are difficult to classify. A similar problem is often encountered in nominally pair-living species where a certain proportion of social units includes an additional adult male or female (e.g., Kappeler and Fichtel 2016). In those cases, a majority

criterion, e.g., > 50, 67, or 75%, seems indicated to characterize the modal social organization, mating, or care system. Species in which otherwise solitary individuals occur only temporarily in association (Psorakis et al. 2015), individuals associate during their period of inactivity and are solitary during their period of activity or vice versa (Kappeler 2012), social organization changes seasonally (breeding pairs vs. winter flocks in some songbirds, Aplin et al. 2015), or were males and females are segregated into different types of social organization for most of the year (Ruckstuhl and Neuhaus 2002; Wearmouth and Sims 2008) pose additional challenges for social taxonomy that still require a general consensus. The framework outlined above may be useful for identifying and defining generally agreed upon criteria.

The evolution of social complexity

Evolutionary questions about social complexity can be grouped into at least four categories. The selective factors that give rise to variation in traits that contribute to social complexity have always been in the focus of behavioral ecologists. More recently, a new line of research has begun to explore the genetic and other proximate mechanisms facilitating or accompanying evolutionary changes in social complexity. Another distinct set of questions deals with evolutionary transitions in traits characterizing social complexity and their co-evolution. Finally, a large body of literature has examined consequences and correlates of variation in social complexity for other traits, especially brain size.

Variation in social systems

First, the selective factors and evolutionary mechanisms giving rise to variation in the core components of social systems have constituted areas of intensive research in behavioral ecology from the beginning (Winn 1958; Klopfer 1962; Crook 1964; Krebs and Davies 1981). Apart from general principles, this line of research also revealed and emphasized taxon-specific factors that influence the balance of the factors that impact variation in the size, composition and spatio-temporal stability of social units. The list of factors that determine whether individuals of a given species live in groups or pairs, or not, is today basic textbook knowledge in behavioral ecology and does not require repetition here (Krause and Ruxton 2002; Davies et al. 2012). Moreover, interspecific variation in social structure has been mainly studied in primates and other mammals, where the nature of food competition as well as phylogenetic similarity have been identified as the most important ultimate determinants of variation in social structure (Sterck et al. 1997; Clutton-Brock and Janson 2012).

Furthermore, the evolution of mating systems has also been a classic topic for behavioral ecologists, who identified the

distribution of receptive females in space and time as fundamental determinants of interspecific variation in mating systems (Emlen and Oring 1977; Greenwood 1980; Thornhill and Alcock 1983; Clutton-Brock 1989; Shuker and Simmons 2014). Which sex, if any, provides parental care is broadly predicted by particular life history constraints defining higher taxa, such as internal vs. external fertilization, ovipary vs. vivipary, litter or clutch size, or lactation, but ecological factors, adult sex ratios, and kinship play additional roles (Clutton-Brock 1991; Reynolds et al. 2002; Hughes et al. 2008; Kokko and Jennions 2008; Gilbert and Manica 2015). Finally, whether allo-parents contribute care for dependent young has also been explained by a combination of life history traits and ecological traits (Rubenstein and Lovette 2007; Hatchwell 2009; Wong and Balshine 2011; Cornwallis et al. 2010; Lukas and Clutton-Brock 2012; Shen et al. 2017). Any modern textbook on animal behavior attest to the enormous progress made towards a detailed understanding of the many causes of variation in social systems and, hence, social complexity across species.

Proximate underpinnings

Second, because social complexity evolves in the sense that it varies systematically among species and higher taxa, its constituent components must have a genetic basis. A fairly recent line of research has therefore begun to illuminate the genomics of social evolution by examining the molecular changes accompanying evolutionary transitions among different types of social organizations (Robinson et al. 2005; Kapheim 2016, 2019). Because an increasing amount of genomic information has become available for hymenoptera and termites, the genomic sources of phenotypic social novelty have primarily been studied by comparing closely related solitary and eusocial insect species (Korb et al. 2015; Kapheim 2016). The key question in this context is whether the evolution of social complexity (or new types of social behavior) relies on genes with new functions, changes in gene regulation, or both (Robinson and Ben-Shahar 2002). Comparative studies across several solitary and eusocial insect species indicated that key changes in gene regulation may have evolved independently in ants and (honey) bees, whereas changes in gene function may have allowed for subsequent taxon-specific social and ecological adaptations (Simola et al. 2013), but across bees, for example, there is no single road map to eusociality, i.e., independent evolutionary transitions in social organization are based on different genetic mechanisms (Kapheim et al. 2015). Interestingly, in bee species with greater social complexity, many important genes show evidence of neutral evolution, indicating relaxed selection. Integration of proposed mechanisms at the genetic, developmental, and behavioral level that accompany changes in social organization is now an exciting task for future research (Rehan and Toth 2015) and one that is

beginning to be addressed in both vertebrates and with respect to physiological mechanisms as well (Rubenstein and Hofmann 2015; Taborsky and Taborsky 2015).

Evolutionary transitions

Third, how social complexity has been modified across time and taxa can be studied by various comparative approaches and methods. A fundamental question in all comparative analyses concerns the degree to which a social trait is correlated to phylogeny. Traits with relatively weak phylogenetic signal are free to vary more in response to ecological and social factors, whereas strongly phylogenetically constrained traits might be less flexible and therefore less likely to increase social complexity (Kappeler et al. 2013). Compared to morphological and physiological traits, behavioral and social traits tend to exhibit relatively weak phylogenetic signal, however (Blomberg et al. 2003; Kamilar and Cooper 2013; Strier et al. 2014). Moreover, reconstructing the presence/absence of an aspect of social complexity on the phylogeny of a given lineage can reveal the directionality of evolutionary transitions and therefore disclose whether social complexity increased (more easily) through certain stepping stones or whether changes in any direction are possible at every speciation event. Such recent analyses revealed, for example, that the evolution of family-living in birds was a pivotal precondition for the subsequent evolution of cooperative breeding (under particular ecological conditions) (Griesser et al. 2017) and that eusocial and communally breeding snapping shrimp evolved independently from pair-living ancestors (Chak et al. 2017).

It is also possible to reconstruct the co-evolution of an aspect of social complexity and a life history or ecological trait to identify preconditions for major shifts in social complexity, and theoretical models can predict certain contingencies in social evolution (e.g., Quiñones and Pen 2017) that can be tested with such comparative studies. For example, in squamate reptiles, vivipary has been a crucial precursor in the evolution of permanent groups containing both adults and juveniles (Halliwell et al. 2017), and in stingless bees, a differentiated soldier caste evolved in association with the appearance of parasitic robber bees (Grüter et al. 2017). In hymenoptera inhabiting an ecological gradient of habitats, ecological constraints and developmental rates were found to predict predominant types of social system at different elevations (Kocher et al. 2014), indicating that different factors promote the emergence of different aspects of social complexity in independent lineages and that we are nowhere near to having a complete list of relevant factors.

A better understanding of the evolution of social complexity can also be achieved by studying the co-evolution of different components of social systems (Elgar 2015). Correlations between group size and the size of a species' vocal repertoire or other communication signals represent

the most commonly studied research question in this context. For example, comparative analyses revealed that among halictid bees, eusocial species have more elaborate sensorial machinery linked to chemical communication than solitary species (Wittwer et al. 2017). There is also evidence suggesting that odor profiles and other aspects of signal complexity may also be more elaborate in eusocial compared to solitary species (Leonhardt et al. 2016; Wenseleers and Zweden 2017). Similar positive relationships between measures of social and communicative complexity have been reported for birds (Krams et al. 2012; Leighton 2017) and mammals (Pollard and Blumstein 2012; Bouchet et al. 2013) and have recently been reviewed elsewhere (Pollard and Blumstein 2012; Peckre et al. 2019, topical collection on Social complexity; see also Pika 2017).

Co-evolution of social systems

Other relationships between different components of a social system are expected, suggesting they also co-evolve together (see also Rubenstein 2012). For example, a given social organization will predict the mating system to some extent—a baboon species living in bisexual groups of 50 individuals is unlikely to be monogamous, for example—and the reproductive consequences of living in single-male or multi-male groups (Davies 2000) or in colonies of single or multiple queens (Keller 1995) have been studied in detail. However, because matings outside the social unit are widespread (Westneat and Stewart 2003; Cohas and Allainé 2009), intraspecific variation in either or both components is common in some lineages (Schradin 2013), and, because some species change their social organization during the breeding season (Wearmouth and Sims 2008), the two components should be conceptually and terminologically separated. Furthermore, the social organization may also predict the care system in some cases—pair-living species are more likely to exhibit biparental care—and the mating system, especially the degree of reproductive skew, may even predicate the type of parental care, particularly the presence of paternal care (Kokko and Jennions 2008), but there is no fixed 1:1 relationship between these two components of a social system (e.g., paternal care is absent in some pair-living species and present in some group-living species; e.g., Tecot et al. 2016). Moreover, interesting relationships between social structure and components of the mating and care systems have been identified that correspond to variation in average levels of kinship among group members (Lukas and Clutton-Brock 2018). Finally, different components of one component of social systems, such as the dispersal regime and grouping patterns, may also not vary independently (e.g., Strier et al. 2014), but such contingencies remain poorly studied. Thus, the fact that the components of a social system do not vary arbitrarily at different levels indicates the existence of multiple mutual contingencies that deserve additional study in the future.

So what?

Finally, whereas social complexity poses many questions that make its study interesting in its own right, the question about its consequences addresses an important conceptual point, namely "Do species differences in social complexity actually matter?" Does the fact that we can rank species according to different levels of social complexity explain or predict anything interesting, or does it simply reflect a human tendency to classify, group and rank natural entities? A more cynical interpretation holds that referring prominently to higher levels of sociality or social complexity may simply be part of a strategy to publish in high-profile journals.

Two interesting consequences of social complexity have been proposed. First, relatively little attention has been given to the notion that "the relationships that result from complex social groups are thought to make possible pro-social behavior like cooperation and reciprocity" (Freeberg and Krams 2015). This hypothesis assumes that communicative complexity increases with social complexity as well as cognitive processing ability in the social domain, including contexts that require or facilitate cooperation. The specific examples presented in favor of this hypothesis so far (Krams et al. 2012) refer to situations in which the recipient of a particular call can benefit from this signal emitted by a group or flock member. More formal comparative tests of this hypothesis might reveal whether the specified links are robust in other taxa and modalities, potentially providing another example of how different components of social systems, in this case two components of social structure as defined and argued above, co-evolve.

Second, the most-studied correlate of social complexity to date is brain size. There are at least five hypotheses that link brain size with some aspect of sociality (Dunbar and Shultz 2017), and all of them assume that the cognitive demands for managing and monitoring social relationships have selected for an increase in the size of the brain or a particular part thereof. While most empirical studies testing these hypotheses have been conducted with birds or mammals (Dunbar and Shultz 2007; Isler and van Schaik 2009; Fox et al. 2017), similar relationships have now also been studied in some invertebrates, where results have been inconsistent (Feinerman and Traniello 2016; Kamhi et al. 2016). These types of comparative studies have been criticized on a number of grounds, however (Healy and Rowe 2007), and brain size variation has recently also been linked to many other factors, including energy (Weisbecker et al. 2015), environmental change (Holekamp and Benson-Amram 2017), and diet (DeCasien et al. 2017). Because many of these studies used group size as the main or only measure of social complexity, future studies using more specific measures of behavioral

complexity and cognitive demands may eventually resolve this question.

Thus, variation in social complexity matters for at least three reasons. First, it provides a framework for the comprehensive and comparative study of sociality. The emergence of sociality represents one of the major transitions in evolution (Maynard Smith and Szathmary 1995), so that studying the evolution of social complexity allows identification of evolutionary principles and patterns, and by exploring the proximate underpinnings of social complexity, we can learn something about control and regulation of complex traits. Second, understanding variation in brain size and the attendant cognitive abilities are major questions in biology that cannot be answered by neuroscientists unfamiliar with the social context in which these traits function and evolve. Finally, species with greater social complexity are also ecologically more successful, as evidenced by termites, hymenoptera, and our own species, lending support to the notion that ecological and social adaptations are closely linked (see also Brooks et al. 2017; Cornwallis et al. 2017).

Conclusions

Social complexity is a key concept in the study of animal and human sociality, but different disciplines and researchers working on invertebrates and vertebrates have used different definitions, concepts, and approaches in the past to study variation in sociality. Humans provide the prime example for intraspecific variation in social complexity, both in space and over time, that has remained virtually neglected in animal studies. Studies of invertebrate societies have always been guided by the notion of different well-defined grades, culminating in eusociality, whereas comparative studies of vertebrate social complexity have relied on various criteria for classifying and ranking species.

It is now generally recognized that social complexity is influenced by both the number of individuals constituting a social unit and their interactions with each other. Building on this insight and acknowledging the various functional components of sociality that have been used for classifying species, I argue that social complexity can be more fully described by reference to social organization, social structure, mating system, and care system. These components of a social system are conceptually and operationally distinct and offer the opportunity to advance comparative studies at all levels by providing a widely applicable social taxonomy that is also amenable to systematic study of the underlying mechanisms, the adaptive value of key social traits, as well as evolutionary transitions among different levels of social complexity.

Compliance with ethical standards

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