

1 Peter M. Kappeler<sup>1,2</sup>, Tim Clutton-Brock<sup>3</sup>, Susanne Shultz<sup>4</sup> & Dieter Lukas<sup>5</sup>

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### 3 **Social complexity: patterns, processes, and evolution**

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5 <sup>1</sup> *Behavioral Ecology & Sociobiology Unit, German Primate Center – Leibniz Institute for*  
6 *Primateology, Göttingen, Germany*

7 <sup>2</sup> *Department of Sociobiology/Anthropology, University of Göttingen, Göttingen, Germany*

8 <sup>3</sup> *Department of Zoology, University of Cambridge, Cambridge, UK*

9 <sup>4</sup> *School of Earth and Environmental Sciences, University of Manchester, Manchester, UK*

10 <sup>5</sup> *Department of Human Behavior, Ecology and Culture, Max Planck Institute for*  
11 *Evolutionary Anthropology, Leipzig, Germany*

12

13 Corresponding author: [pkappel@gwdg.de](mailto:pkappel@gwdg.de)

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27 **Abstract**

28 Animal and human societies exhibit extreme diversity in the size, composition and cohesion  
29 of their social units, in the patterning of sex-specific reproductive skew, in the nature of  
30 parental care, in the form and frequency of cooperation and in their competitive regime,  
31 creating a diversity of socially complex societies. However, there is an ongoing debate about  
32 whether social complexity is a real, emergent property of a society or whether it only provides  
33 a conceptual framework for studying the diversity and evolution of societies. In this  
34 introduction to our topical issue, we identify three areas of current research addressing  
35 relevant challenges in the study of social complexity. First, most previous studies have  
36 ignored intraspecific variation, and the proximate and ultimate determinants of variation in  
37 social complexity, as well as their interactions, remain poorly known. Second, previous  
38 studies have suffered from a lack of a common conceptual framework, including shared  
39 definitions, and existing measures of social complexity do not acknowledge its multiple  
40 components and dimensions. Third, comparative studies of social complexity offer  
41 opportunities to explore its biological causes and correlates and but it is frequently difficult to  
42 identify the causal relationships involved and the development of general insights has been  
43 hampered by conceptual and methodological difficulties. In this paper, we briefly characterize  
44 these three challenges and offer guidance to the other contributions to this topical collection  
45 on social complexity by placing their key results in the context of these three topics.

46

## 47 **Introduction**

48 Animal societies exhibit fascinating diversity in the size, composition and cohesion of their  
49 social units, in the patterning of sex-specific reproductive skew, in the nature of parental care,  
50 in the form and frequency of cooperation and in their competitive regime (Clutton-Brock  
51 2016, Rubenstein and Abbot 2017a). Variation in social systems has often been ranked or  
52 ordered along gradients to facilitate comparisons of the relative complexity of different  
53 societies (e.g., Sherman et al. 1995, Bourke 1999, Anderson and McShea 2001, Whitehead  
54 2008, Avilés and Harwood 2012, Rubenstein et al. 2016, Rubenstein and Abbot 2017a, Lukas  
55 and Clutton-Brock 2018), and to explore relationships between measures of social complexity  
56 and interspecific variation in cognition (Barrett et al. 2007, Healy and Rowe 2007, Dunbar  
57 and Shultz 2017) or communication (Blumstein and Armitage 1998, Freeberg et al. 2012,  
58 Pika 2017). However, it is still an open question whether social complexity is a property of a  
59 society that is measurable on a single scale and whether it is useful to attempt to compare the  
60 complexity of different societies.

61 A fundamental problem is that social complexity has proved difficult to define and  
62 operationalize (Freeberg et al. 2012, Bergman and Beehner 2015, Fischer et al. 2017). In  
63 some cases, biologists have regarded more complex societies as those simply consisting of  
64 many individuals (Dunbar 1992, Anderson and McShea 2001, Freeberg et al. 2012); others  
65 have regarded more complex societies as those where groups are comprised of social roles,  
66 such as multiple breeding females, breeders and non-breeding workers or helpers, or members  
67 of morphologically different castes (Anderson and McShea 2001, Groenewould et al. 2016,  
68 Rubenstein and Abbott 2017b). Yet others regard complex societies as those where social  
69 groupings can be identified at multiple levels (Whitehead 2008). Finally, some regard  
70 complex societies as those where social relationships between group members are  
71 individually differentiated (Bergman and Beehner 2015). Different indices of complexity are  
72 not necessarily correlated with each other: indeed, one recent analysis of measures of social  
73 complexity across mammals showed that two common measures of social complexity (the

74 extent to which group members occupy functionally different roles and the complexity of  
75 interactions between dyads) are negatively correlated with each other (Lukas and Clutton-  
76 Brock 2018)

77         As a result, it is still uncertain whether it is either possible or useful to compare the  
78 overall complexity of different societies and there is a need to examine the usage and  
79 distribution of specific social traits used to estimate complexity and their relationships to each  
80 other. In this paper, we briefly outline some of the current key questions and topics in the  
81 study of social complexity, thereby providing a context for the other contributions to this  
82 topical collection.

83

#### 84 **Concepts and methods for studying social complexity**

85 Characterizing social complexity is fraught with practical and conceptual problems. A main  
86 practical problem in this context is due to the fact that both historically and taxonomically,  
87 different traits have been used to characterize or rank the degree of social complexity of  
88 different taxa (Kappeler 2018, topical collection on Social complexity, Lukas and Clutton-  
89 Brock 2018). In this context, it remains an open question whether it is possible to construct a  
90 single index of social complexity that can be applied across taxonomically diverse species or  
91 whether different indices of social complexity have to be used in different lineages.

92         Because comparisons of single traits do not capture all dimensions of social  
93 complexity recognized in different studies, multiple aspects of complexity need to be  
94 considered whenever possible. It is consequently necessary to decide what range of measures  
95 should be included in both single and comparative studies. It might even be feasible to  
96 combine several measures into a single estimate of social complexity (see Turchin et al.  
97 2018). Conceptual clarity about relevant measures of social complexity and their inter-  
98 dependence is therefore an important prerequisite for comparative research.

99           Several contributions to this topical issue contribute theoretically or empirically to  
100 recent attempts at better describing patterns of social complexity. Kappeler (2018, topical  
101 collection on Social complexity) critically reviews definitions and previous studies of social  
102 complexity in invertebrate and vertebrate societies, and defines social organization, social  
103 structure, mating system and care system as distinct components of any species' social  
104 system. He argues that recognition of these four components might offer a framework for  
105 comprehensive and comparative studies of social complexity that ought to be useful for future  
106 studies.

107           Aureli and Schino (2018, topical collection on Social complexity) add an important  
108 perspective by arguing that the study of social complexity can be either based on how it is  
109 perceived from the outside or on how it is experienced from within, i.e., how individual group  
110 members may experience and perceive the complexity of their social interactions. Focusing  
111 on the latter perspective, they propose that variation between and within social relationships,  
112 variation in opportunities to interact with different group members and the variable role of  
113 third parties generate species differences in experienced social complexity that may also  
114 inform future studies of social cognition.

115           The contribution by Weiss et al. (2018, topical collection on Social complexity) deals  
116 with the practical challenges of measuring social complexity. They propose a new method for  
117 examining the complexity of animal social networks based on association indices, which can  
118 reflect different types of dyadic relationship within a social network. Using binomial mixture  
119 models, they examine the performance of this measure with simulated and real data sets, and  
120 they outline additional approaches that build on interaction rate and multidimensional  
121 relationship data.

122           Wilkinson et al. (2018, topical collection on Social complexity) also use social  
123 network analyses, but in combination with genetic data, to determine whether kinship  
124 explains the highly variable patterns of association found among bats. Using all available  
125 empirical data, they find that most species show evidence of emergent social organization.

126 Specifically, sex-biased dispersal gives rise to interspecific variation in the number of  
127 relatives across social units, and bat species in which individuals change roosts frequently  
128 tend to exhibit higher levels of association among female relatives. Because the existence of  
129 dominance hierarchies and various types of cooperation are independent of the patterns of  
130 relatedness across species, the authors conclude that kinship is not a prerequisite for social  
131 complexity in bats.

132 Finally, Storms et al. (2018, topical collection on Social complexity) present empirical  
133 data on complex patterns of collective motion exhibited by starlings under attack by a raptor.  
134 Collective movements represent one dimension of social organization that can exhibit highly  
135 complex dynamics in large animal schools, flocks or herds. Based on time-series analyses the  
136 authors show that the specific type of collective escape in the three-dimensional environment  
137 of their particular study system depends both on the collective pattern that precedes it and the  
138 level of threat posed by the raptor.

139

#### 140 **Variation in social complexity**

141 Social complexity – however measured – is highly variable across species, which differ in  
142 group size, adult sex ratios, and in the nature and patterning of associations and social  
143 relationships, for example. Questions concerning the distribution as well as the determinants  
144 of this variation are either in the focus of current research or represent important open  
145 questions for future research.

146 First, variation in the components of social systems remains poorly studied. Except for  
147 human societies, we know surprisingly little about the magnitude of intraspecific variation in  
148 different social traits across populations of the same species inhabiting different habitats,  
149 among neighboring groups within a population, or within groups over time (but see Lott 1991,  
150 Richards et al. 2003, Jones et al. 2007, Schradin 2013). Moreover, different components of  
151 social systems appear to have different phylogenetic inertia (Kamilar and Cooper 2013,

152 Kamilar and Baden 2014), but the nature and magnitude of this variation remains to be  
153 systematically explored. For example, whether a species exhibits only maternal or paternal,  
154 biparental, cooperative or no parental care does not seem to vary much within species or even  
155 genera and families (Clutton-Brock 1991, Shultz et al. 2011), whereas intraspecific variation  
156 in aspects of social organization, like group size and composition, appears to be common and  
157 widespread (e.g., Lott 1991, Schradin 2013, Garber et al. 2016, Agnani et al. 2018).  
158 Systematic description of the patterning of intra- and interspecific variation among traits  
159 characterizing social organization, social structure as well as the mating and care system  
160 would seem to provide a basis for both, attempts at better describing social complexity of a  
161 given species and for better characterizing mean tendencies of particular traits used in  
162 comparative analyses.

163         Second, much remains to be learned about the factors driving variation in traits  
164 contributing to measures of social complexity and their interaction. For example, the study of  
165 molecular pathways proximately mediating the control of traits used to assess aspects of  
166 social complexity, like alloparental care, from genome structure and gene expression patterns,  
167 through epigenetic and developmental processes to mechanisms of neuroendocrine regulation  
168 and neural circuits, has so far been largely limited to a few insect model systems (Robinson et  
169 al. 2005, Rubenstein and Hofmann 2015, Kapheim 2016, Dogantzis 2018) and should clearly  
170 be expanded to suitable vertebrate species.

171         Recent comparative studies revealed that various ecological and life history variables  
172 also impact measures of social complexity. For example, the evolution of cooperative  
173 breeding in mammals has been restricted to lineages where females produce multiple  
174 offspring per birth, mating systems are monogamous and average coefficients of relatedness  
175 between group members are relatively high (Lukas and Clutton-Brock 2012, 2018). Similarly,  
176 evolutionary transitions from family units to cooperative breeding in birds are associated with  
177 higher environmental uncertainty (Jetz and Rubenstein 2011) and shifts to habitats with more  
178 variable productivity and more pronounced seasonality (Griesser et al. 2017). In shrimp,

179 ecological generalism is associated with evolutionary transitions to eusociality (Brooks et al.  
180 2017), indicating that sociality is shaped by various ecological factors.

181         Several contributions to this topical issue address relevant topics in this context. He et  
182 al. (2018, topical collection on Social complexity) emphasize the role of the physical  
183 configuration of habitat features in shaping the social organization and social structure of  
184 group-living animals. The logic of their argument involves two steps: by shaping individual  
185 decisions about when and where to move, the physical environment impacts which  
186 individuals aggregate or encounter one another, and thus their propensity to interact with each  
187 other. The authors summarize published studies supporting this neglected perspective and  
188 present analytical approaches based on social network measures that can identify and quantify  
189 the effects of habitat configuration on social organization and social structure.

190         Two other contributions to this topical issue highlight the effects of social variables  
191 and mechanisms on social complexity, focusing on evolutionary changes and contemporary  
192 variation in humans, respectively. van Schaik et al. (2018, topical collection on Social  
193 complexity) highlight the importance of cumulative culture, which relies fundamentally on  
194 social learning, in generating social and cultural complexity in humans. Exploiting various  
195 sources of data, the authors argue that the complex forms of cumulative culture characterizing  
196 modern humans depended on the simultaneous emergence of language and an increase in  
197 proactive cooperation. According to their analyses, the more recent explosive diversification  
198 of human social complexity and material culture was triggered by an increase in novelty-  
199 seeking, which first facilitated the dramatic range expansions by our ancestors into highly  
200 divergent types of habitats and later the emergence of agriculture. This paper therefore nicely  
201 emphasizes the temporal dimension of changes in social complexity that is typically not  
202 accessible in studies of animal behavior.

203         The contribution by Naess et al. (2018, topical collection on Social complexity)  
204 highlights variation in one aspect of human social complexity (cooperative decision-making)  
205 within and across populations. Using gift games to probe cooperative tendencies among

206 pastoralists from independent populations, the authors found that most variance in gift-giving  
207 between study sites was due to differences in the importance of relatedness and reciprocity.  
208 Their study also illustrates complex interactions among social organization and social  
209 structure that may also be found in some animal societies.

210         Biologically relevant variation in social complexity must ultimately be accompanied  
211 by changes in the genetic underpinnings of the relevant traits. Taking an exemplary  
212 comprehensive perspective, Kapheim (2018, topical collection on Social complexity) reviews  
213 recent findings regarding the mechanisms, ontogeny, evolution, and function of social  
214 complexity in hymenopterans. Most of our current understanding of the genetic bases of traits  
215 impacting social systems is based on studies of members of this lineage, and this contribution  
216 provides a welcome accessible introduction to this topic. It is also becoming increasingly  
217 apparent that developmental plasticity, e.g., maternal or sibling effects on development, are  
218 major drivers of caste-related behavior, i.e., social cues also act as proximate determinants of  
219 social variation. How social and molecular traits interact to generate variation and ultimately  
220 evolutionary change in social complexity in vertebrates is a frontier in the study of sociality  
221 (Rubenstein and Hofmann 2015) that will be informed and inspired by the existing body of  
222 research summarized in Kapheim's paper.

223

#### 224 **Evolutionary changes in social complexity**

225 It is equally interesting to explore the evolutionary correlates and consequences of changes in  
226 measures of social complexity and other traits, such as cognitive abilities, brain size or  
227 communication signals. We have already emphasized the importance of choosing clearly  
228 defined variables representing variation in social complexity for both, assembling data sets  
229 with high internal validity for comparative studies based on multiple published sources and  
230 for meaningful comparison across studies of different taxa or independent studies of the same  
231 lineage (see also Borries et al. 2016, Lukas and Clutton-Brock 2017, Schradin 2017). A

232 second prerequisite concerns the quality of the phylogenetic information that is used to either  
233 reconstruct ancestral states and trait evolution or to control for phylogenetic non-  
234 independence as well as choosing appropriate comparative methods (Garamszegi 2014).

235 In terms of the biologically important questions in this context, there has been  
236 discussion of (i) which traits constitute components of social complexity and which ones are  
237 independent of each other, (ii) whether components of social complexity vary categorically or  
238 continuously across species, (iii) the direction(s) of causality in any co-evolutionary pattern  
239 detected through comparative analyses, and (iv) the relative importance of any singular  
240 measure of social complexity in explaining variation in a given other trait of interest.

241 The remaining contributions to this topical issue address at least one of these issues in  
242 this very active field of research. Peckre et al. (2018, topical collection on Social complexity)  
243 revisit the relationship between social and communicative complexity. Several, but not all,  
244 previous studies had suggested that animals living in more complex social environments also  
245 have communication repertoires with more and/or more complex signals. The authors first  
246 establish problems with the operationalization of measures of both variables, including the  
247 neglect of the multi-modal nature of most social communication, that may have contributed to  
248 equivocal outcomes across studies. They go on to emphasize the importance of also  
249 considering alternative hypotheses to social complexity in explaining co-variation in other  
250 traits; in this case the relative roles of ecology, morphology and phylogenetic history in  
251 driving signal complexity. As indicated by their discussion of the intimate relationships  
252 between social context, including the presence of variable audiences, and signaling behavior,  
253 one may even question the conceptual separation between social and communicative  
254 complexity (as also argued by Kappeler 2018, topical collection on Social complexity).

255 By detailed comparisons at two levels, i.e., between different social contexts of signal  
256 production and between closely-related species, Gustison et al. (2018, topical collection on  
257 Social complexity) provide an example of how differences in social organization and social  
258 structure between two species of Old World monkeys are accompanied by changes in their

259 respective vocal repertoires. Geladas, which live in very large groups, produce vocalizations  
260 in long sequences, especially when levels of conspecific noise are high. Sequence complexity,  
261 but not duration, increase when males approached females to initiate social interactions. Thus,  
262 compared to chacma baboons, the change in social organization (group size) and social  
263 structure (cross-sex bonds) towards more complexity has led to corresponding changes in  
264 vocal complexity. The exact co-evolutionary dynamics, i.e. “have changes in X permitted,  
265 facilitated, driven or followed changes in Y?”, remain also obscure at this very detailed level  
266 of comparison, however.

267         The contribution by Boucherie et al. (2018, topical collection on Social complexity)  
268 emphasizes the value of in-depth study of other taxa exhibiting interesting variation in social  
269 complexity and cognitive abilities apart from primates. Reviewing decades of research on  
270 natural social dynamics and experimentally-probed social-cognitive skills of ravens, the  
271 authors show how these traits co-vary. Their focus on a comprehensive set of studies  
272 conducted on this single species also leads them to emphasize the importance of how being  
273 intimately familiar with a particular species can improve the detail and biological relevance of  
274 questions about the evolution of social complexity being asked.

275         The contribution by Gonzales and Martins (2018, topical collection on Social  
276 complexity) focuses on the analytical methods used in studies of the evolution of social  
277 complexity and its co-evolution with other traits. They briefly review some of the advances  
278 and pitfalls in the statistical approaches underlying such analyses. They then illustrate the  
279 usefulness of a new method by analyzing two aspects of social complexity in primates:  
280 variation in group size as a function of activity pattern and habitat use and variation in mating  
281 systems driving the evolution of baculum length. Thus, this paper also illustrates that aspects  
282 of social complexity co-evolve with many other traits and that they can be treated as both  
283 independent or dependent variables.

284         Taken together, the contributions to this topical collection on social complexity sketch  
285 a representative picture of the diversity of questions and approaches in current research on

286 this topic. We hope that this topical issue will stimulate additional research on key problems  
287 in the study of animal and human societies within the framework of social complexity.

288

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