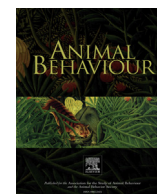




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Measuring social complexity

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In one of the first formulations of the social complexity hypothesis, Humphrey (1976, page 316, *Growing Points in Ethology*, Cambridge University Press) predicts 'that there should be a positive correlation across species between *social complexity* and *individual intelligence*'. However, in the many ensuing tests of the hypothesis, surprisingly little consideration has been given to measures of the independent variable in this evolutionary relationship, that is, social complexity. Here, we seek to encourage more rigorous measures of social complexity. We first review previous definitions of this variable and point to two common flaws; a lack of objectivity and a failure to directly connect sociality to the use of cognition. We argue that, rather than creating circularity, including cognition in the definition of social complexity is necessary for accurately testing the social complexity hypothesis. We propose a new definition of social complexity that is based on the number of differentiated relationships that individuals have. We then demonstrate that the definition is both broadly applicable and flexible, allowing researchers to include more detailed information about the degree of differentiation among individuals when the data are available. While we see this definition of social complexity as one possible way forward, our larger goal is to encourage researchers examining the social complexity hypothesis to carefully consider their measurement of social complexity.

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If you say that someone 'lacks social skills', this is an unambiguous insult that reveals a fundamental feature of how we think about social cognition; being social requires certain abilities that are beyond the reach of some people. In addition to informing how we think about other people, this idea forms the basis for evolutionary ideas about social cognition across species. The social complexity hypothesis (independently arrived at by Jolly (1966) and Humphrey (1976)) posits that sociality is cognitively challenging and, consequently, drives cognitive evolution. As an evolutionary hypothesis, the social complexity hypothesis can be tested by making comparisons across species, ideally using comparative methods that control for the pattern of relatedness among the species in the sample (MacLean et al., 2012). As Humphrey (1976, page 316) states, the hypothesis 'demands that there should be a positive correlation across species between *social complexity* and *individual intelligence*'. Indeed, in the nearly 40 years since Humphrey's statement, numerous studies have reported exactly such a relationship. For example, across primate species there is a well-known correlation

between the size of the social group (used as an indicator of social complexity) and the relative size of the neocortex (used as an indicator of intelligence, Dunbar, 1995).

As this example demonstrates, testing the social complexity hypothesis across species requires quantifying (or at least ranking) both the 'social complexity' and the 'individual intelligence' of species. Certainly, there has been extensive debate about how to measure 'intelligence' (or cognition, e.g. Healy & Rowe, 2007), the dependent variable in Humphrey's stated relationship above. Indeed, broad comparisons using crude measures such as brain size are increasingly being replaced or augmented with more targeted comparisons among closely related species that compare experimentally assessed cognitive performance (Bond, Kamil, & Balda, 2003; MacLean et al., 2013). However, despite urgings by Healy and Rowe (2007) and others (e.g. Holekamp, 2007) to improve measures of 'social complexity' (the independent variable in the relationship), there has been considerably less progress in this area. Indeed, we are struck that, despite dissatisfaction with the most widely used measure of social complexity (group size; e.g. Shultz & Dunbar, 2007), an alternative has yet to be widely adopted. Moreover, all measures currently employed have flaws, being either too subjective or only tangentially related to social cognition.

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Therefore, our goal in this manuscript is primarily to encourage more objective and systematic measurements of social complexity. After reviewing previous measures, we propose a new measure of social complexity based on the *number of differentiated relationships* that members of a species have with conspecifics. We demonstrate how this definition can be expanded to facilitate finer-grained comparisons when more detailed data are available. Finally, we illustrate how this definition can be applied using three examples.

TERMINOLOGY

There are several different terms for evolutionary hypotheses that connect sociality and cognition: ‘the social complexity hypothesis’ (e.g. Connor, Smolker, & Richards, 1992), ‘the social brain hypothesis’ (e.g. Dunbar, 1998), ‘the social intelligence hypothesis’ (e.g. Kummer, Daston, Gigerenzer, & Silk, 1997) and ‘the Machiavellian intelligence hypothesis’ (e.g. Byrne & Whiten, 1988). Although research under each hypothesis may emphasize different aspects of sociality or cognition (e.g. only the Machiavellian hypothesis emphasizes deception as a key component; Byrne & Whiten, 1988), they are nevertheless all similar in that they propose a causal evolutionary link from sociality to cognition. Here, we use the term ‘social complexity hypothesis’ because it is broadly applicable and because it places emphasis where we feel it should be placed; that is, on the independent variable in the relationship, sociality. This emphasis avoids logically confounding the independent (sociality) and dependent (cognition) variables. In practice, it can be difficult to completely separate the independent and dependent variables because over shorter timescales the causation can go in the other direction: greater cognitive ability may enable more complex social interactions.

COMPLEXITY

It is perhaps also worth considering the broader issue of complexity. Although easy to intuit, the term ‘complexity’ itself is difficult to quantify. Most attempts to quantify complexity focus on either the number of parts in a system, the relationship between the parts, or both. For example, the definition of McShea and Brandon (2010, page 7) captures both of these concepts: ‘the number of part types or degree of differentiation among parts’. Definitions of social complexity have also tended to focus on these two concepts (more parts, or more differentiation between parts) with varying degrees of explicitness. For example, the widely used variable ‘group size’ directly measures the number of parts in the system.

PREVIOUS MEASURES OF SOCIAL COMPLEXITY

Social Features as Indicators of Complexity

A common way to compare social complexity across species is to use particular aspects of sociality as indicators of complexity. For example, a species with a linear dominance hierarchy may be more socially complex than a species that lacks a dominance hierarchy (Maclean, Merritt, & Brannon, 2008). Other features that have been used to indicate social complexity include: pair bonds (Shultz & Dunbar, 2007), complex alliances (Connor, 2007), flexible nesting strategies (Tibbetts, 2004), foraging as a permanent flock (Bond et al., 2003), social transactional interactions (Burish, Kueh, & Wang, 2004), a lack of reproductive skew (Pawłowski, Lowen, & Dunbar, 1998), tactical deception (Byrne & Corp, 2004) and crèches (Krasheninnikova, Bräger, & Wanker, 2013). Although this approach appears an objective one, the use of arbitrary features can be quite subjective. With a limited number of species, it is nearly

always possible to identify one particular social feature that corresponds to greater (or lesser) cognitive ability. Thus, in the absence of any a priori reason to consider a social feature as cognitively challenging, this method makes it difficult to falsify the hypothesis. This problem is exacerbated if the social feature is not clearly defined. For example, as pointed out by Beauchamp and Fernández-Juricic (2004), the use of ‘transactional’ interactions as an indicator of complex bird societies by Burish et al. (2004) does not clearly relate to published accounts of each species’ sociality. Instead, the variable appears to allow large-brained (but mostly solitary) birds such as woodpeckers (Picidae) to count as socially complex (Beauchamp & Fernández-Juricic, 2004). Furthermore, the social features typically used in such comparisons are often only tangentially (if at all) related to cognition. For example, while forming crèches sets the stage for more complex social interactions in parrots (Krasheninnikova et al., 2013), there is little social cognition inherent in crèche formation; it merely requires attraction to other nests and tolerance of other offspring. Without some direct link to cognition, comparative patterns linking social features to cognition may be entirely spurious. Moreover, noncognitive definitions of sociality put researchers at risk of missing actual correlations between sociality and cognition in their taxa.

Qualitative Comparisons of Social Systems

Rather than identifying a particular social feature as an indicator of social complexity, some researchers have made qualitative comparisons across different types of social systems. For example, fission–fusion societies have been suggested to be more complex than other vertebrate societies (Amici, Aureli, & Call, 2008; Aureli et al., 2008). Fission–fusion societies with multiple levels may be even more complex (Couzin, 2006). Conversely, in bats, stable groups may be more complex than unstable groups because they are more likely to involve cooperative behaviours (Wilkinson, 2003). Within ungulates, monogamy has been proposed as more complex than alternative mating patterns (Shultz & Dunbar, 2006). Conversely, in primates, multimale systems may be more complex than the alternatives (Shultz & Dunbar, 2007). Yet, this approach is also subject to the aforementioned problems; (1) researchers may be tempted to retro-fit the social system ranking to the cognitive data in hand, and (2) they may do so with no grounding in cognition. As such, sociocognitive relationships may not be detected accurately.

Quantitative Comparisons of Social Systems

Many researchers rely on quantitative comparisons of social features across species, comparing species based on the number of X, with X being some social variable. The most common such variable is the number of individuals in a social unit (group size, e.g. Dunbar, 1995), but other variables include grooming clique size (Kudo & Dunbar, 2001), colony size (Wilkinson, 2003), or the number of demographic roles (Blumstein & Armitage, 1998). Quantitative measures are a dramatic improvement over other measures because they are objective and avoid issues of circular reasoning. Quantitative comparisons have an inherent order to them because complexity increases with more ‘parts’. Thus, quantitative comparisons are less fungible than qualitative ones. However, quantitative comparisons are still susceptible to finding spurious correlations; or, equally problematic, can obscure true relationships because the measured social variable has no direct relationship to cognition. For example, the use of group size has been criticized because it obscures underlying variation in how animals are interacting within those groups (Shultz & Dunbar, 2007).

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