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Communication as a Fundamental Part of Machiavellian Intelligence

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The Machiavellian intelligence hypothesis proposes that individuals in complex social groups require sophisticated social cognition. This hypothesis has advanced our understanding of the complex social lives of animals and how individuals interact with others in their groups. Machiavellian intelligence is the capacity of an individual to alter the behavior of others around it to the individual's own advantage. This capacity is typically facilitated by complex communicative systems, social systems, and cognitive abilities. Curiously, communication among group members has not traditionally been a focus of research related to the Machiavellian intelligence hypothesis. Here, we show how a focus on communicative and cognitive complexity together can elucidate nuanced manipulations for selfish gains in socially complex groups, under both competitive and cooperative scenarios. Finally, we argue more generally that a research emphasis on communication in complex social groups may accelerate our understanding of the social mechanisms underlying complex adaptive behavior.

Keywords: communication, cooperation, Machiavellian intelligence, social cognition, social complexity

Effective and efficient social living requires social cognition in many animal species (Marino, 2017). Social cognition can include a wide range of processes, such as the ability to recognize group members, remember past interactions, and strategically influence the behavior of others (Shettleworth, 2010). The capacity of an individual to alter the behavior of others around it to the individual's own advantage is known as Machiavellian intelligence, or more broadly as one of the types of social intelligence (Byrne & Whiten, 1988, 1997; Dunbar, 1998; see Dunbar and Shultz (2017) for a recent review of different social intelligence hypotheses). Communication is the primary tool animals use to effect this process of altering others' behavior to their own advantage (Freeberg, Dunbar, & Ord, 2012), as animals influence the behavior of others through signaling. Moreover, communicative diversity will influence the amount and precision of information that can be conveyed by an individual, as outlined in the social complexity hypothesis for communication (Freeberg et al., 2012). Furthermore, individuals in complex social groups should be more effective at assessing the behavior of others, including both signals that have evolved to function in communication between individuals and cues that have not evolved for that communicative function (but are byproducts of other behavior or physiology; Maynard Smith & Harper, 2003). Nonetheless, communication, signals, and cues involved in interactions among individuals are rarely a focus of studies of Machiavellian intelligence.

Of growing interest are the evolutionary and functional relationships between social cognition, social complexity, and communicative systems. Increased social cognition is hypothesized to occur in species with more complex social groups (discussed in detail in the following text), compared with solitary species or those with simpler social groups (Byrne & Whiten, 1988, 1997; de Waal & Tyack, 2003; Sewall, 2015; Shultz & Dunbar, 2007). In comparison with relatively simple social groups, complex social groups represent greater uncertainty for individuals in those groups in terms of the diversity of individuals any animal may interact with, the context of that interaction, and what that individual's behavior will be in response to the interaction. Species with complex social groups are, in turn, expected to have complex systems of communication, providing individuals with diverse means to assess and manage the behavior of others in their groups (Dunbar, 2003; Freeberg et al., 2012).

Both communicative and social complexity can be emergent properties of higher organizational scales. For example, an ant lays a simple chemical trail when coming back from a newly detected food source (Gordon, 2010). Other individuals will then follow the trail, allowing the colony as a whole to exploit the food resource.

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However, the ants start to seek other food resources (or to engage in other tasks) as the resource is depleted and, as a result, the original chemical trail dissipates with less use. Each individual may follow a single and simple behavioral rule, but complex and adaptive group-level behavior emerges.

Krause, James, Faria, Ruxton, and Krause (2011) showed clearly that we can say the same for problem-solving, and perhaps even more generally about adaptive patterns of social behavior (Puga-Gonzalez & Sueur, 2017). This is important because the implied level of organization of the Machiavellian intelligence hypothesis is at the individual level, not at the group level. Individuals in many social species have advanced cognitive skills that are selected for by their more complicated levels of sociality. This complex sociality, in turn, selects for advanced levels of communicative skills in individuals. However, a close analysis of each of these three pillars of the Machiavellian intelligence hypothesis (social cognition, social complexity, and communication) suggests that we need to be careful about how the hypothesis is framed, or perhaps step back and try to understand if the scope of the hypothesis is such that it deals with phenomena that only exist at the individual level. We also feel that it is important to treat Machiavellian intelligence related to cooperative interactions separately from Machiavellian intelligence related to competitive interactions because the role of communication under these two circumstances is quite different.

Here, we propose a conceptual framework for studying the relationships between communication, social complexity, and social cognition under two scenarios of Machiavellian intelligence (Figure 1). We begin by describing social and communicative complexity, and how these types of complexity link to social cognition. We base our descriptions on the definition used by the majority of researchers who have thus far published on social and communicative complexity—more components (individuals or signals) make for larger systems (group size or signal repertoires), and "more" is generally more complex than "less," particularly if each component is found at about the same frequency (Freeberg et al., 2012; Pollard & Blumstein, 2012). We note here that complex systems have a large number of diverse and interacting units that can adapt to environmental changes (broadly defined) and that are not absolutely predictable (Page, 2011). Finally, we also explain the importance of the organizational scale and finish with a discussion of the cooperative versus competitive sides of Machiavellian intelligence.

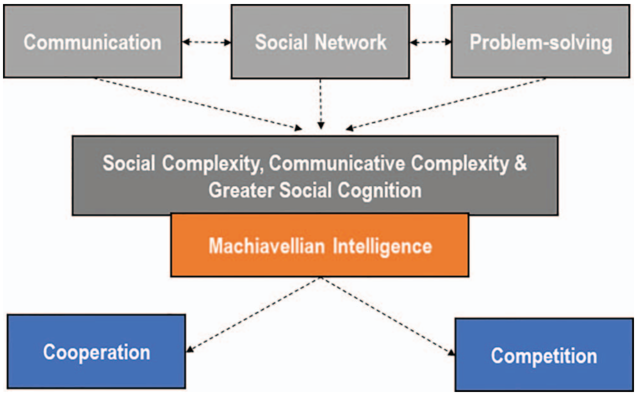

Figure 1. Conceptual framework for studying Machiavellian Intelligence. Emergent properties of communities and social groups (top) synergistically drive complexity of sociality and communication. These in turn allow for the expression of Machiavellian intelligence. Machiavellian intelligence is exhibited under two different contexts: cooperation and competition. See the online article for the color version of this figure.

Communicative, Social, and Cognitive Complexity

Communicative Complexity

A starting point to the question of signal complexity is information. We might generally think of a biological system as being complex if it contains or processes a large amount of information. From the classic information-theoretical approach of Claude Shannon (Shannon & Weaver, 1949), a system with a large amount of information is one that has high entropy (or uncertainty, in communication terms). A system with high entropy can be thought of as one with a large number of parts, where each of these parts interacts/interconnects with all other parts with roughly equal probability. If one were to pick a single part from such a system (call this the current state of the system), it would be difficult to guess which part was chosen. Thus, one could conclude that the current state of the system has a high level of uncertainty or entropy. Similarly, if the system itself was a communicative system in which the expression of a part correlates with some state of interest, systems with high entropy have the capacity to convey a broad range of information because the occurrence of any given part can greatly reduce the level of uncertainty about state. Alternatively, a system with low entropy may have a similar number of parts, but perhaps only a small number of those parts regularly occur or act, and perhaps only interact or interconnect regularly with a few other parts. Thus, if the occurrence of the next part in a series is highly predictable, its expression will not convey much new information about state.

Using entropy as a basis, we can view signaling complexity simply as the number and diversity of elements in a system. Quoting McShea (2005, p. 150), we can view complexity as the "amount of differentiation among parts, where variation is continuous, or as number of part types, where variation is discrete" (Harrison & Klein, 2007; McShea & Brandon, 2010). Entropy metrics have been used for decades as measures of complexity in signaling systems, and new approaches extending these earlier measures are being developed and validated (Kershenbaum, 2014; Kershenbaum et al., 2016).

McShea's diversity approach is a powerful way for testing broad evolutionary ideas related to complexity. However, elements in any system can contribute to complexity over different scales. For example, linkage between elements can provide hierarchical levels of complexity (Page, 2011). The English language is an obvious example with letters nested in words nested in paragraphs nested in chapters nested in books. Bird song offers a nonhuman example of this (Catchpole & Slater, 2008). Single sounds (notes) are nested within clusters of notes (syllables, trills, etc.) nested within phrases nested within songs nested within longer bouts of songs and other vocalizations. Moreover, the spectral properties of animal vocal signals provide a range of information about the signaler identity, sex, social status, or geographical origin of the signaler (Zimmermann, 2017).

Three other design features that potentially affect signaling complexity include (a) syntax, (b) redundancy, and (c) multidimensionality and multimodality:

(1) Syntactically complex communicative systems can use two different types of syntax. Phonological syntax conveys information from combinations of phonemes. For example, words in language are constructed from phonemes, each of which does not specifically convey information, but together they convey the information embedded in the word. Animal systems that have analogous structures include the prairie dog (*Cynomys gunnisoni*) alarm calls (Slobodchikoff & Placer, 2006) and the chick-a-dee call system of many species of the family Paridae (Freeberg & Lucas, 2012; Krams, Krama, Freeberg, Kullberg, & Lucas, 2012). Lexical syntax describes how elements, each of which is capable of carrying information, combine to transmit additional or new information relative to the component elements (Arnold & Zuberbühler, 2006; Crockford & Boesch, 2005; Engesser, Ridley, & Townsend, 2016; Hobaiter, Byrne, & Zuberbühler, 2017; Suzuki, Wheatcroft, & Griesser, 2016). Syntactical rules allow a signaler to encode more information than would otherwise be transmitted with single elements only. Syntactical rules include variation in the diversity of elements used to construct a signal in addition to the rate at which elements are emitted (Engesser, Ridley, & Townsend, 2017; Ouattara, Lemasson, & Zuberbühler, 2009).

(2) Theoretically, redundancies in communicative systems reduce information flow rates because different elements are designed to carry the same information instead of all elements carrying different information. Nonetheless, redundancies are common (Bradbury & Vehrencamp, 2011). Redundancy often makes functional sense related to either fundamental needs of information transmission or physiological/anatomical constraints on signal production. For example, Carolina chickadees, *Poecile carolinensis*, regularly use chick-a-dee calls to communicate a wide range of social functions (Krams et al., 2012). Calls vary considerably in note composition, different note compositions are used in different contexts, and fine acoustic structure of individual notes is often predictive of the number of other notes in the calls (Freeberg, Lucas, & Clucas, 2003). Thus, if a chickadee heard only part of a chick-a-dee call of another individual, it might still be able to gain the general meaning of the complete call. Ay, Flack, and Krakauer (2007) showed that an optimal level of redundancy can result from a tradeoff between specificity (i.e., maximal entropy) and robustness (i.e., maximal decoding of a signal). The optimal level of the tradeoff will be determined by the noise level imposed on the system—higher levels of noise require higher levels of redundancy for robust information transfer. Results from a number of studies support this prediction. For example, chaffinches (*Fringilla coelebs*) in noisier environments sing longer bouts of a specific song before switching to a new song type (Brumm & Slater, 2006), western grebes (*Aechmophorus occidentalis*) increase the number of advertising calls in noisier environments (Nuechterlein & Buitron, 2006), and king penguins (*Aptenodytes patagonicus*) increase the number of contact calls and the number of syllables per call in windy compared with calmer conditions (Lengagne, Aubin, Lauga, & Jouventin, 1999). Here "noise" also extends to receiver physiology. For example, certain avian mobbing calls are produced at specific frequencies and specific amplitude modulation rates to which a wide variety of songbirds are maximally sensitive (Henry, Gall, Velez, & Lucas, 2016).

(3) One conclusion that can be drawn from patterns of redundancy is that environmental and physiological constraints will limit the capacity of complex communicative systems to carry information. However, signals can be designed to carry more information by increasing the dimensionality of signal elements (Nelson & Marler, 1990) and by producing signal elements that carry information received across multiple sensory modalities (Partan & Marler, 1999; Ronald, Fernandez-Juricic, & Lucas, 2012). For example, visual signals can carry more information by increasing the number of colors or the shapes of color patches. Vocal signals can carry more information by adding frequency or amplitude modulations, or by adding harmonics to a tone. Chemical signals can carry more information when mixtures of chemicals are added together. Different dimensions of a signal can also provide additional levels of redundant information and thereby increase signal robustness. For example, the spectral properties of the first notes in a chick-a-dee call are predictive of the syntax of the entire call (Freeberg et al., 2003), thus increasing the probability that the syntactical information is decoded correctly by the receiver.

Multimodal signals are extraordinarily common. As with multidimensionality, different components of a signal designed to stimulate different sensory modalities in the receiver can either enhance robustness by increasing redundancy (e.g., waving and drumming display of fiddler crab species of genus *Uca*; Mowles, Jennions, & Backwell, 2017) or enhance information bandwidth by allowing for nonredundant channels of information flow (e.g., brown-headed cowbirds, *Molothrus ater*, song and mating dance; Ronald, Zeng, White, Fernandez-Juricic, & Lucas, 2017).

Overall, communicative systems can be used by receivers to decode a tremendous amount of information about a wide variety of contexts, and they can be used by signalers to convey that information to alter the behavior of receivers. Moreover, the entire communicative process can be more complicated when multiple individuals are part of the communication network. The number and diversity of individuals that may be part of a communication network is dictated in part by the social complexity of the group.

Social Complexity

Tests of the social complexity hypothesis for communication have used a variety of different definitions of social complexity.

Some authors have suggested that group size is a reasonable index of social complexity (Street, Navarrete, Reader, & Laland, 2017; Vonk, 2016; Zimmermann, 2017), with the caveat that the group is not considered "social" if it is a simple aggregation around some resource (e.g., food or water) or forms due to some short-term external stimulus (e.g., predators). At the least, there should be some level of individual (Roberts & Roberts, 2016; Sewall, 2015) or group (Boughman & Wilkinson, 1998; Price, 1999; Tyack, 2008; Yurk, Barrett-Lennard, Ford, & Matkin, 2002) recognition that would facilitate stable social relationships among group members.

However, a consensus has formed more recently among authors contributing to this literature who suggest that group size is not a sufficient measure of social complexity. Instead, social complexity is seen as a combination of group size and the complexity of social relationships within the group (Borrego & Gaines, 2016; Fischer, Farnworth, Sennhenn-Reulen, & Hammerschmidt, 2017; Pollard & Blumstein, 2012; Roberts & Roberts, 2016; Sewall, 2015). The social relationships that contribute to social complexity include the diversity of behavior patterns exhibited in a social context, relative interaction frequency, number of alliances, number of different social roles, and the number of differentiated relationships (i.e., the number of individuals treated differently by a focal animal; Bergman & Beehner, 2015). Freeberg et al. (2012) added unit density to this list, suggesting that individuals that are on average closer together will interact more intimately and at higher rates. Freeberg et al. (2012) also included egalitarian dominance structure, suggesting that a strong hierarchy may limit the strength of relationships between unit members. Fission–fusion dynamics of the social groups under study will also affect the social complexity of the group (Aureli et al., 2008).

The organization and integration of interactions between individuals within a group will often have adaptive value to group members. In many social species, the group serves group members, but group members also serve the group. This parallels general systems thinking that the system exists as a result of the parts, and the parts exist as a result of the system (Meadows, 2008). Relative to simple groups (let alone solitary individuals), complex groups have more, and more diverse, members that have more, and more diverse, interconnections among one another. It is important to point out, though, that even fairly solitary species can be found in social networks of varying social complexity (Freeberg et al., 2012). For example, solitary male lizards with smaller home ranges interact with a wider number of neighbors than those with larger home ranges (Ord, Blumstein, & Evans, 2002).

Generally, then, complexity in groups is seen in "more is more complex" terms. Compared with simpler groups, more complex groups have more individuals, a greater diversity of individuals, and more connections among individuals (Pollard & Blumstein, 2012; Whiten, 2000). This view of complexity is similar to the notion of Shannon entropy discussed earlier. One reason to take this entropy view of complexity is that it is close to the idea at the heart of the word complexity—an interweaving of parts to make a complex whole, and a functioning and flexible/adaptive whole when it comes to animal groups. More (and diverse) connections among the many parts of a system generate a more interwoven and intertwined system than one with similar parts but fewer connections (McShea, 1996, 2005). Second, from the standpoint of an individual animal in such a network, having to interact with more individuals in its group and in a wider range of contexts (affiliation, aggression, movement, cooperation, competition, etc.) is more complex than having to interact with few individuals in its group (Barrett, Henzi, & Lusseau, 2012). Stated differently, seen from the individual's standpoint, a highly connected network is more complex in part because the next interaction is less predictable on a moment-to-moment basis, as is the next individual's behavioral response to the interaction.

A useful way to deal with interconnectedness of group members is through the use of social network approaches (Croft, James, & Krause, 2008; Krause, James, Franks, & Croft, 2015; Kulahci, Rubenstein, & Ghazanfar, 2015; Scott, 2012; Snijders & Naguib, 2017). We briefly summarize three basic measures that have value relative to the question of social complexity, though there are *many* others. The first measure, called network or edge density, relates to connectedness. For a network of a certain number of individuals (each called a node), the network density is the proportion of connections among individuals that exist (the edges among network nodes) relative to the total number of connections that could exist given the number of individuals. For example, a group of yellow-bellied marmots, *Marmota flaviventris*, in which each individual interacted regularly with all other individuals, would have a network density of 1, whereas a group of marmots in which pairs of individuals only ever interacted with each other would have a network density closer to 0. Network density has functional significance, for example, having been found to relate to seasonal changes in reproduction and rearing of the young in rhesus macaques, *Macaca mulatta* (Brent, MacLarnon, Platt, & Semple, 2013).

A second basic network measure relates more directly to the question of possible information flow within a network. This information flow measure is called the average network path length or the network's diameter (Lusseau, 2003). The path length for two individuals in a network is the minimum number of connections (edges) that are required to get from one individual to the second. Path lengths among individuals, and the average path length of the network as a whole—its diameter, are useful "global" measures of the network because they tell us generally how close two individuals in a network are to each other. An average path length of 1, as an obvious example, would mean that each individual in the group was directly linked to every other individual in the group. We mentioned the importance of path length in terms of information flow—a message (say, about the location of a resource or the detection of a predator) should flow more rapidly through the network if the path lengths are shorter than if they are longer. Like density, network path lengths are biologically meaningful. For example, they are diminished by removal of certain individuals in the network of bottlenose dolphins, *Tursiops truncatus* (Lusseau, 2003). Furthermore, simulations based upon data from 30 primate species indicate that path lengths influence the transmission of information through these systems (Kasper & Voelkl, 2009; Voelkl & Noe, 2010; see also Pasquaretta et al., 2015 for a relationship among the efficiency of information flow in groups of primates and social cognition). Information flow in common ravens (*Corvus corax*) is similarly affected by social centrality in the network and by affiliative links in particular (Kulahci et al., 2016).

The third basic network measure we consider is clustering. The clustering coefficient of a network captures local connectedness. In a group of animals, this is a measure of the number of individuals that are one connection away from other individuals (e.g., the number of nodes one edge away from each node in the network) and of how many of the potential "triangles" of interconnections among the three individuals in that space occur. The average clustering coefficient for the network is the mean clustering coefficients of each individual, ranging from 0 (*no "triangles" of interconnections among triads of individuals*) to 1 (*all possible "triangles" of interconnections among triads of individuals occur*). Networks with a clustering coefficient near 1 therefore exemplify networks where an individual's closest relations are also highly connected with one another. Like the other two network measures we discussed, clustering coefficients in networks are functionally significant. For example, clustering coefficients decline as a result of the introduction of parasite-infected individuals in experimental groups of guppies, *Poecilia reticulata* (Croft et al., 2011), and predict initiators and receivers of fin-related injuries in Atlantic salmon, *Salmo salar* (Cañon-Jones, Noble, Damsgard, & Pearce, 2011). Indeed, clustering seems one of the core features of social networks that differentiates them from nonsocial networks (Easley & Kleinberg, 2010).

The Link Between Social Cognition, Communication, and Sociality

More complex communication and heightened social cognition (or the knowledge about conspecifics; Seyfarth & Cheney, 2015) are to some extent correlated properties that are selected for in complex social systems compared with relatively simple social systems (Fischer et al., 2017). Greater communicative complexity is associated with a greater ability to modify the behavior of others in social systems. For example, only the social African mole rat species of the family Bathyergidae have contact calls (used to facilitate cooperative behavior), and social species have more distress calls than solitary species (Vanden Hole, Van Daele, Desmet, Devos, & Adriaens, 2014). As another example, grooming networks are strongly correlated with calling networks in social lemurs of the family Lemuroidea (Kulahci et al., 2015); grooming relationships are a strong index of social ties in lemurs, thus the implicit link between communication and social systems.

Similarly, social cognition will typically be associated with levels of social complexity (Bergman & Beehner, 2015). This association can be due to greater social cognition, which makes more complex social interactions possible, or the association could be due to socially complex environments requiring an individual's understanding the status, roles, signaling reliabilities, interactions, and relationships of other individuals in the group (Seyfarth & Cheney, 2015). Dwarf mongooses, *Helogale parvula*, for example, give alarm calls in response to immediate threats (Collier, Radford, Townsend, & Manser, 2017). However, false alarms are common enough that it is important for the receiver of the alarms to evaluate their saliency. Kern, Laker, and Radford (2017) showed that dwarf mongoose receivers respond more intensely to calls by individuals who act as sentinels compared with calls from other individuals in the group. As expected, sentinels are in the best position to evaluate the true risk involved. Domestic chickens, *Gallus gallus*, illustrate well-known audience effects in which sender communication is predicated on who else is around to hear a signal (Marino, 2017). For example, costly aerial alarm calls are more likely to be given in the presence of a female the male has mated with than in the presence of a female the male has not mated with, suggesting alarm calling functions not in mate attraction but in mate investment (Wilson & Evans, 2008). Chickens also give food calls and displays used to attract females. The vigor of the calls and displays is correlated with the quality of the food and the probability that a female will be attracted to the site (Marler, Dufty, & Pickert, 1986).

Problem-solving and innovation in humans (Bahrami et al., 2010) and in nonhuman animals (Reader, Morand-Ferron, & Flynn, 2016) are other key aspects of cognition that appear to be enhanced in more complex social systems, particularly if the problems relate to the social domain (Holekamp, Dantzer, Stricker, Shaw Yoshida, & Benson-Amran, 2015). For example, cognitive innovation is correlated with mean group size in primates (Sewall, 2015). Naïve great tits, *Parus major*, and blue tits, *Cyanistes caeruleus*, solve foraging-related problems more rapidly in larger flocks, and in particular in flocks with experienced birds (Morand-Ferron & Quinn, 2011). This latter finding underscores the importance of the "pool of competence" hypothesis for social cognition. This hypothesis states that larger groups are more likely to contain individuals who are competent at specific tasks, which in turn makes the group as a whole more competent at solving a variety of problems. Increased diversity in groups can also influence the problem-solving abilities of group members. A recent study of mixed-species flocks facing a novel feeder task revealed that chickadees and titmice in flocks with greater mixed-species flock diversity were more likely to solve the novel feeder task than birds in less diverse flocks (Freeberg, Eppert, Sieving, & Lucas, 2017). Such benefits of diversity in groups may be particularly true for humans, where individual performance at problem-solving can be uncorrelated with group-level performance (Krause et al., 2011).

The importance of social cognition in complex social systems suggests that individuals in complex social groups will face selection pressure for increased neural substrate (e.g., structure, density, interconnections) for processing more sophisticated social information compared to solitary individuals or individuals in simple social groups. This view has come to be known as the social brain hypothesis (Dunbar, 2003; Humphrey, 1976; Jolly, 1966) and has support from comparative work (Aiello & Dunbar, 1993; Dunbar, 2009; Dunbar & Shultz, 2017; Pérez-Barbería, Shultz, & Dunbar, 2007; Walker, Burger, Wagner, & Von Rueden, 2006). There is also some experimental evidence suggesting that increases in group size select for larger neocortex volumes and increased neural activity in the neocortex in rhesus macaques, *Macaca mulatta* (Sallet et al., 2011).

Other work has called the social brain hypothesis into question, however (Barrett, Henzi, & Rendall, 2007; Healy & Rowe, 2007; Powell, Isler, & Barton, 2017). For example, comparative studies find greater support for alternative hypotheses such as diet or hunting style (DeCasien, Williams, & Higham, 2017; MacLean, Barrickman, Johnson, & Wall, 2009), or mating system and courtship behavior (West, 2014), playing a stronger role than social complexity in explaining neural variation. Moreover, processing of social information may not be as cognitively demanding in animals (including humans) as many authors have argued (Alexander, 1974). Social cognition may ultimately require at minimum that individuals possess a general social pattern recognition to navigate their social worlds effectively. Such pattern recognition may represent a relatively simple mechanism to explain putatively complex cognitive processes such as coalition formation and reconciliation (Barrett et al., 2007; discussed in the following text in more detail).

Regardless of the neural mechanisms of processing social information, individuals in more complex social groups require greater communicative complexity in comparison with individuals in relatively simple social groups. There should be a greater need for sensitivity to changes in social context in complex groups, and an individual may have to adjust signal use quickly in light of those changes. This ability to adjust signals quickly has long been documented in avian and primate species (Catchpole & Slater, 2008; Liebal, Waller, Burrows, & Slocombe, 2014), and recent evidence from playback experiments reveals a similar ability in Mexican free-tailed bats, *Tadarida brasiliensis* (Bohn, Smarsh, & Smotherman, 2013).

Our argument is also agnostic to particular definitions of communication. We view communication in the widely held sense of the transfer of messages or information from a sender to a receiver (Bradbury & Vehrencamp, 2011). Over the years, this view has been criticized for its reliance on information and the "conduit metaphor" of signalers packaging information into the signals that they direct to receivers (Burghardt, 1970; Owings & Morton, 1998; Rendall, Owren, & Ryan, 2009). These anti-information approaches view communication as the means to "achieve fitness-enhancing ends by influencing the behavior of others, in part by exploiting their assessment systems" (Owings & Morton, 1998, p. 29). These anti-information views have themselves been criticized (Seyfarth et al., 2010; Stegmann, 2013). Ultimately for our arguments, the particular definition of communication does not matter. Although we take an information approach to communication in our discussion throughout this paper, our arguments about social complexity driving communicative complexity could be made using language of researchers from the anti-information camp. Individuals in complex social groups should possess more complex systems of communication, either to influence the behavior of diverse others more effectively or to convey a wider range of messages to diverse others in their groups, or both, in comparison with individuals in simple social groups. Indeed, despite their antagonism to the notion of information in communication, both Morton (1977) and Owings and Morton (1998) have argued that complexity in social groups should influence the diversity and complexity of communication patterns in those groups.

Organizational Scales of Complexity

Signals have the capacity to transmit a tremendous amount of information across a broad range of categories of message (Fedurek, Zuberbühler, & Dahl, 2016; Marino, 2017; Pollard & Blumstein, 2012; Zimmermann, 2017). Signal redundancy can increase the level of robustness of information transfer from sender to receiver. In addition, the coevolution between signal design and receiver physiology plays an important role in robust information transfer (Henry et al., 2016). Enhanced cognition may also be a critical part of the capacity of a complex communicative system to carry information. However, one component of this viewpoint that is often underappreciated is the organizational scale over which complexity is realized.

Signal complexity may differentially reflect complexity at the individual, group, or even colony level. For example, ID signatures can be designed to carry more or less information depending on the dimensionality of the signal (Beecher, 1989), but the realization of that complexity occurs at the group or population level. Similarly, certain social systems may require that each individual convey information across a variety of contexts, thus requiring high signal complexity at the individual level. Alternatively, if the social roles in a social network limit the range of contexts over which an individual shares information, either resulting from sharp differences in a dominance hierarchy (Freeberg & Lucas, 2012) or resulting from qualitatively different social roles filled by individuals of different ages (as is common in social insects; Leonhardt, Menzel, Nehring, & Schmitt, 2016), then there may be little signal complexity at the individual level compared with signal complexity expressed at the group or colony level.

Social complexity may also be expressed at the individual level or may be an emergent property of the group. As we suggested earlier, social complexity is related to the diversity of behavior patterns, number of different social roles, and number of differentiated relationships in a group. As such, social complexity is, by these measures, an emergent property by definition. This is important for several reasons. From the perspective of information flow (and therefore of communicative complexity), individuals in confined roles may be constrained in the breadth of information they share, and therefore in the breadth of signals they transmit to convey that information. We can say the same thing about the cognitive correlates of socially complex groups: Individuals may not need to solve a variety of problems if these social roles constrain the range of problems faced by any given individual. As such, the group as a whole may have complex signaling properties and complex problem-solving capacities, but this range of problem-solving skills may not extend down to the level of the individual. Social insects provide an extreme example of this where a small behavioral repertoire at the individual level can result in a sophisticated array of behaviors expressed at the colony level (Anderson, Franks, & McShea, 2001; Anderson & McShea, 2001; Gordon, 2010). These scaling issues may be important in the evolution of Machiavellian intelligence, as we discuss in the following text.

The basis of the Machiavellian intelligence hypothesis is twofold. One fundamental idea is that animals manipulate other animals socially in a way that benefits the manipulator. This manipulation is typically effected through communication, though communication per se has rarely been the focus of studies of Machiavellian intelligence. The second fundamental idea is that the ability of the signaler to manipulate the receiver is enhanced by the signaler's knowledge of the cognitive state of the receiver—and hence through social intelligence (Kershenbaum & Blumstein, 2017). We (and many others) have argued that complex social systems select for complex communicative systems that are needed to convey information between individuals in the social networks and that social cognition is selected for because the depth of problems imposed by the social system can be more complex than those imposed by the environment (Freeberg et al., 2012).

The Cooperative Side of Machiavellian Intelligence

The negative connotations implied by the invocation of Machiavellian intelligence notwithstanding, this type of intelligence applies to both cooperative and competitive interactions (Figure 2; van Schaik, Isler, & Burkart, 2012). The expectation for cooperative interactions is that the change in behavior induced in the receiver should be advantageous for both receiver and sender. The expectation for the competitive interactions is that the change in behavior induced in the receiver should be advantageous for the sender but represent a net cost to the receiver. We treat these two sides of Machiavellian intelligence separately because the expected role of communication is quite different between them. The cooperative side potentially requires a full range of information exchange and therefore a complex communicative system to facilitate that exchange (Cronin, 2012; Freeberg & Krams, 2015; Kershenbaum & Blumstein, 2017). The competitive side often results from deceptive or false signals that effectively parasitize an existing signaling system. As we discuss in the following text, perceptual bias (Ryan & Cummings, 2013) should be a primary driving force for this competitive side of Machiavellian intelligence, which may have little relevance for communicative complexity per se.

We see the evolution of complex communicative systems as an inevitable outcome of selection pressures stemming from the requirements of living in complex social systems (Freeberg et al., 2012; Pollard & Blumstein, 2012). However, the relationship between signal complexity and social complexity potentially exists at different levels in different taxa. As discussed earlier, the social insects are a perfect example of this. Communicative complexity is greater in insects with more complex social systems (Leonhardt et al., 2016), but these patterns are shown at the colony level in insects, not at the individual level. In contrast, Machiavellian intelligence relates to interactions that occur between individuals and assumes that the individuals know each other well enough to estimate each other's cognitive states or at least to the extent that each individual knows how to modify others' behavior to its own advantage. We pointed out that the density of social units and the level of egalitarianism in social units are indices of social complexity (Freeberg et al., 2012). These traits should also facilitate high levels of information transfer across a diversity of contexts, and this trait in turn selects for communicative complexity at the individual level. Thus, communication—and by extension complexity within communicative systems—is a critical element of the cooperative side of Machiavellian intelligence.

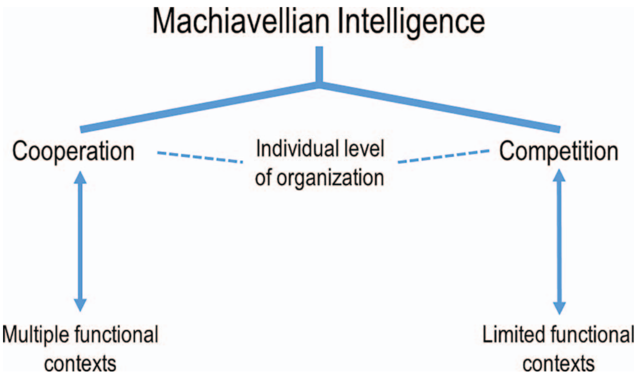

Figure 2. Machiavellian intelligence is expressed under two conditions, cooperative and competitive. Both conditions work at the organizational scale of the individual. Cooperative Machiavellian intelligence works under multiple functional contexts, whereas competitive Machiavellian intelligence works under a limited range of contexts. The consequences of this difference are discussed in the text. See the online article for the color version of this figure.

The role that social relationships play relative to Machiavellian intelligence is illustrated in the pied flycatcher (*Ficedula hypoleuca*; Krama et al., 2012). Breeding flycatchers on nesting territories are attracted to the location of a low-level predator through mobbing calls generated by the resident male. The function of the mob is to drive away the predator. Birds from neighboring territories will always join the mob, but birds from more distant territories only join the mob if the resident male has previously joined a mob on the territory of the potential responder (Krama et al., 2012). Thus cooperative behavior mediated by a vocal signal is conditional on the level of past cooperation in the social network.

Chimpanzees (*Pan troglodytes*) provide an important example of the cooperative side of Machiavellian intelligence that underscores the role of communicative complexity in social cooperation. Chimpanzees use a variety of different call systems under different contexts. The rough grunt call is a food call that attracts other individuals to the presence of food (Schel, Machanda, Townsend, Zuberbühler, & Slocombe, 2013). This food call can be produced along a graded continuum where acoustically distinct variants are elicited by food types that vary in quality (Slocombe & Zuberbühler, 2006). Another call, the pant hoot, is a vocalization given under a wide variety of contexts. One role of the pant hoot is to facilitate reunions with other members of the social network, particularly in males (Fedurek, Donnellan, & Slocombe, 2014). Schel et al. (2013) showed that pant hoots from a specific individual played back to a silently feeding chimp were more likely to elicit a rough grunt (food call) from the silent feeder when there was a high level of friendship between the pair and when the simulated approaching individual (i.e., emitter of the pant hoot) was of higher rank than the forager. The point here is that the level of cooperation is dependent on memory of past social affiliations and relative dominance rank. Moreover, the cooperation is mediated by two call systems, at least one of which also conveys properties that provide for individual recognition.

Our final example under the cooperative side of Machiavellian intelligence is particularly intriguing because it incorporates elements of both the cooperative side and competitive side of Machiavellian intelligence. Fork-tailed drongos, *Dicrurus adsimilis*, associate with mixed-species flocks of birds. They use several vocal systems to influence heterospecific individuals in these flocks. One vocalization is a true drongo alarm call used to warn others about a predator, and one is a false alarm call, mimicked from another species, that is used to flush individuals away from food items that the drongo will then retrieve (Flower, 2011). Aspects of the latter are discussed in the next section on the competitive side of Machiavellian intelligence. A third vocalization is a nonalarm sentinel call (Baigrie, Thompson, & Flower, 2014). On hearing this sentinel call, species associated with the drongo will increase their foraging behavior and decrease vigilance (Baigrie et al., 2014). The drongos will only give this sentinel call in the presence of other species, not when they are alone. In other words, the expression of this signal is associated with an audience effect. Drongos will also give this sentinel call after they have used the false alarm call to kleptoparasitize food from a heterospecific. The result is that the heterospecific will resume foraging sooner than it would without the sentinel call, decreasing the cost of responding to the false alarm call. Thus, both the true drongo alarm call and the sentinel calls, given in social settings, provide benefits to both the drongo and to the heterospecific. In contrast, the false alarm call is strictly manipulative, reflecting the competitive side of Machiavellian intelligence. We turn to that topic now.

The Competitive Side of Machiavellian Intelligence

Here we focus on competitive aspects of the Machiavellian intelligence hypothesis and specifically where communication fits in with the ability of a signaler to manipulate the behavior of the receiver to the signaler's advantage and to the receiver's disadvantage. As a shorthand, we will call this deceptive signaling, where a sender sends a false or deceptive signal about something so that the sender can take some advantage of the receiver's response. We characterize deception as the production of a signal that causes the receiver to respond appropriately to some state that is encoded in the signal, when in fact that state does not currently exist (Weldon, 2017). In other words, the signaler lies or exaggerates about some important environmental or physiological state that is relevant to the receiver.

Deceptive signaling itself is both common and shown across a broad range of taxa, from bacteria that withhold quorum sensing molecules, to orchids that mimic female wasps to entice male wasps to pollinate them, to Batesian mimics whose signals imply that they are toxic when they are not (Mokkonen & Lindstedt, 2016; Weldon, 2017). In each of these cases, the sender is essentially parasitizing a communicative system by falsely advertising the information encoded in the parasitized signal. However, these particular examples fall outside of the concept of Machiavellian intelligence because they do not involve social cognition—as they are not examples of flexible, tactical deception, but rather fixed characteristics of the organism (Byrne & Whiten, 1988). Examples that do fall under the competitive side of the Machiavellian intelligence also exist. For example, lower ranking tufted capuchin monkeys, *Cebus apella*, give false alarm calls more often when there is contestable food available that dominants could control (Kean et al., 2017; Wheeler, 2009). Male chickens will give food calls in the absence of food to attract potential mates, and the females will stop responding if the males repetitively lie (Marino, 2017). Fork-tailed drongos use false alarm calls to kleptoparasitize food items that they typically are incapable of obtaining themselves from pied babblers and meerkats (Child, Flower, & Ridley, 2012; Flower, 2011). Male topi antelopes, *Damaliscus korrigum*, alarm snort when there are no predators in the area in order to retain a female in their territories (Bro-Jørgensen and Pangle, 2010).

These cases that appear to fall under Machiavellian intelligence possess a number of similarities. First, the context of the parasitized signal is highly relevant to the receiver. Contexts include immediate predation risk or access to limited food resources. This means that there is a cost to ignoring the deceptive signal (Mokkonen & Lindstedt, 2016). Second, the fitness consequences associated with the context of these signals are strong enough that we should expect receivers to have a perceptual bias for detecting them. For example, alarm calls used by birds in the family Paridae are broadcast at high frequencies (Ficken, 1990). Moreover, the species for which we have data for auditory processing show that their high frequency hearing is unusually sensitive compared with "normal" songbirds (Henry & Lucas, 2008). Both the saliency of the context and the perceptual bias for these signals in the receiver should make the signals easily falsified. Third, there is no selection for complexity in the signal used to deceive the receiver. Instead, there is selection for the sender producing a relatively simple and highly salient signal that will result in a predictable response by the receiver. Fourth, the organizational scale of these signals is designed to work at the level of the individual. Predator alarm calls in particular should be designed to encode information for a broad range of receivers, irrespective of any role that the receivers play in the social unit. In other words, the perceptual bias should be a general property of any of the members of the social unit. As such, drivers of signal design for the competitive side of Machiavellian intelligence should be narrow in context with a strong perceptual bias, whereas drivers of signal design for the cooperative side of Machiavellian intelligence should be broader in context and associated with a complex signaling system. These patterns are particularly clear with approaches that emphasize the role of communication in complex social groups.

Conclusions

The Machiavellian intelligence hypothesis has advanced our understanding of the social lives of animals (including our own species) and how individuals negotiate adaptively with others in their groups (Byrne & Whiten, 1988; Byrne & Whiten, 1997). Work in this field has increased our understanding of how individuals that must rely heavily on interactions with other members of their social groups can sometimes gain fitness benefits by behaving selfishly—often by manipulating the behavior of others using communicative signals. Despite this focus on manipulation, however, communication among group members curiously has not traditionally been a focus of work on Machiavellian intelligence.

We have focused our arguments here on vocal signaling, as this is the modality of communication we have studied the most (and is also the main modality that has been studied in light of the social complexity hypothesis for communication; Freeberg et al., 2012). However, we could have made the same arguments with other modalities. Visual signaling—such as visual displays, facial expressions, and gestures—is the second most common type of communication considered by researchers testing relationships between social complexity and signaling complexity. Comparative studies indicate that individuals in more complex social groups have more, or more complex, facial markings in *Polistes* wasps (Tibbetts, 2004), visual displays in Agamidae and Iguanidae lizards (Ord et al., 2002), facial expressions in nonhuman primates (Dobson, 2009), and facial and bodily gestures in *Macaca* species (Maestripieri, 2005). Indeed, in communication in nonhuman primates, gestural signaling is essential for an individual to modify the behavior of others effectively (Graham, Furuichi, & Byrne, 2017; Hobaiter et al., 2017; Hobaiter, Leavens, & Byrne, 2014; Roberts, Vick, & Buchanan-Smith, 2013).

We see several questions as ripe for testing to advance our knowledge of the role of communication in social intelligence. Here we suggest a few. Geographical variation in behavior within species is observed in a wide range of species and for a wide range of behavioral systems (Foster & Endler, 1999). Does intraspecific variation in group size reliably predict variation in signaling complexity? Does variation in signaling complexity reliably predict variation in key aspects of Machiavellian intelligence such as tactical deception? Artificial selection experiments in species with short generation times could determine whether selection for greater social complexity (perhaps via social network analysis metrics) produces individuals with greater communicative complexity. If so, does such artificial selection also generate individuals with a more sophisticated way of manipulating the behavior of others? Artificial selection for brain size in guppies led to females and males with larger (selection up lines) and smaller (selection down lines) brain sizes than the founder population, in just two generations, and large-brained females solved discrimination tasks better than small-brained females (Kotrschal et al., 2013; but see Healy & Rowe, 2013). Finally, it seems surprising that so little attention has been focused on the level of organization (e.g., individual vs. group) relative to the social complexity hypothesis for communication, or of the consequences of organizational level on any of the pillars of Machiavellian intelligence we discuss here. A clear discussion of these consequences would be quite valuable in this literature.

We hope that our brief review will trigger a greater interest in communication for research in this field. We have drawn connections among three features of life fundamental to many social animal species: complexity of the social group, communicative systems, and social cognition. We have also proposed a conceptual framework that considers organizational scale and circumstance of Machiavellian intelligence. We now hope that future research on the processing of social information in complex social groups will focus on communicative interactions in greater detail. Such research would benefit from testing signal variation and complexity from the standpoint of signalers living in complex social groups and also from testing how individuals effectively assess the signals and cues of others in those groups.

References

Aiello, L. C., & Dunbar, R. I. M. (1993). Neocortex size, group size, and the evolution of language. *Current Anthropology, 34,* 184–193. http://dx.doi.org/10.1086/204160

Alexander, R. (1974). The evolution of social behavior. *Annual Review of Ecology and Systematics, 5,* 325–383. http://dx.doi.org/10.1146/annurev.es.05.110174.001545

Anderson, C., Franks, N. R., & McShea, D. W. (2001). The complexity and hierarchical structure of tasks in insect societies. *Animal Behaviour, 62,* 643–651. http://dx.doi.org/10.1006/anbe.2001.1795

Anderson, C., & McShea, D. W. (2001). Individual versus social complexity, with particular reference to ant colonies. *Biological Reviews of the Cambridge Philosophical Society, 76,* 211–237. http://dx.doi.org/10.1017/S1464793101005656

Arnold, K., & Zuberbühler, K. (2006). Language evolution: Semantic combinations in primate calls. *Nature, 441,* 303. http://dx.doi.org/10.1038/441303a

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., . . . van Schaik, C. P. (2008). Fission-fusion dynamics: New research frameworks. *Current Anthropology, 49,* 627–654.

Ay, N., Flack, J., & Krakauer, D. C. (2007). Robustness and complexity co-constructed in multimodal signalling networks. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences, 362,* 441–447. http://dx.doi.org/10.1098/rstb.2006.1971

Bahrami, B., Olsen, K., Latham, P. E., Roepstorff, A., Rees, G., & Frith, C. D. (2010). Optimally interacting minds. *Science, 329,* 1081–1085. http://dx.doi.org/10.1126/science.1185718

Baigrie, B. D., Thompson, A. M., & Flower, T. P. (2014). Interspecific signalling between mutualists: Food-thieving drongos use a cooperative sentinel call to manipulate foraging partners. *Proceedings of the Royal Society B: Biological Sciences, 281,* 20141232. http://dx.doi.org/10.1098/rspb.2014.1232

Barrett, L., Henzi, P., & Rendall, D. (2007). Social brains, simple minds: Does social complexity really require cognitive complexity? *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences, 362,* 561–575. http://dx.doi.org/10.1098/rstb.2006.1995

Barrett, L., Henzi, S. P., & Lusseau, D. (2012). Taking sociality seriously: The structure of multi-dimensional social networks as a source of information for individuals. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences, 367,* 2108–2118. http://dx.doi.org/10.1098/rstb.2012.0113

Beecher, M. D. (1989). Signaling systems for individual recognition: An information-theory approach. *Animal Behaviour, 38,* 248–261. http://dx.doi.org/10.1016/S0003-3472(89)80087-9

Bergman, T. J., & Beehner, J. C. (2015). Measuring social complexity. *Animal Behaviour, 103,* 203–209. http://dx.doi.org/10.1016/j.anbehav.2015.02.018

Bohn, K. M., Smarsh, G. C., & Smotherman, M. (2013). Social context evokes rapid changes in bat song syntax. *Animal Behaviour, 85,* 1485–1491. http://dx.doi.org/10.1016/j.anbehav.2013.04.002

Borrego, N., & Gaines, M. (2016). Social carnivores outperform asocial carnivores on an innovative problem. *Animal Behaviour, 114,* 21–26. http://dx.doi.org/10.1016/j.anbehav.2016.01.013

Boughman, J. W., & Wilkinson, G. S. (1998). Greater spear-nosed bats discriminate group mates by vocalizations. *Animal Behaviour, 55,* 1717–1732. http://dx.doi.org/10.1006/anbe.1997.0721

Bradbury, J. W., & Vehrencamp, S. L. (2011). *Principles of animal communication* (2nd ed.). Sunderland, MA: Sinauer.

Brent, L. J. N., Maclarnon, A., Platt, M. L., & Semple, S. (2013). Seasonal changes in the structure of rhesus macaque social networks. *Behavioral Ecology and Sociobiology, 67,* 349–359. http://dx.doi.org/10.1007/s00265-012-1455-8

Bro-Jørgensen, J., & Pangle, W. M. (2010). Male topi antelopes alarm snort deceptively to retain females for mating. *American Naturalist, 176,* E33–E39. http://dx.doi.org/10.1086/653078

Brumm, H., & Slater, P. J. B. (2006). Animals can vary signal amplitude with receiver distance: Evidence from zebra finch song. *Animal Behaviour, 72,* 699–705. http://dx.doi.org/10.1016/j.anbehav.2006.01.020

Burghardt, G. M. (1970). Defining "communication". In J. W. Johnston Jr., D. G. Moulton, & A. Turk (Eds.) *Advances in chemoreception, Vol. 1: Communication by chemical signals* (pp. 5–18). New York, NY: Apple-ton-Century-Crofts. http://dx.doi.org/10.1007/978-1-4684-7155-7_2

Byrne, R. W., & Whiten, A. (1988). *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans*. New York, NY: Oxford University Press. Retrieved from http://psycnet.apa.org/record/1988-98392-000

Byrne, R. W, & Whiten, A. (Eds.). (1997). Machiavellian intelligence. *Machiavellian intelligence II: Extensions and evaluations, Machiavellian intelligence* (pp. 1–23). Cambridge, United Kingdom: Cambridge University Press. http://dx.doi.org/10.1017/CBO9780511525636

Cañon-Jones, H. A., Noble, C., Damsgard, B., & Pearce, G. P. (2011). Social network analysis of the behavioural interactions that influence the development of fin damage in Atlantic salmon parr (*Salmo salar*) held at different stocking densities. *Applied Animal Behaviour Science, 133,* 117–126. http://dx.doi.org/10.1016/j.applanim.2011.05.005

Catchpole, C. K., & Slater, P. J. B. (2008). *Bird Song: Biological themes and variations* (2nd ed.). Cambridge, NY: Cambridge University Press. http://dx.doi.org/10.1017/CBO9780511754791

Child, M. F., Flower, T. P., & Ridley, A. R. (2012). Investigating a link between bill morphology, foraging ecology and kleptoparasitic behaviour in the fork-tailed drongo. *Animal Behaviour, 84,* 1013–1022. http://dx.doi.org/10.1016/j.anbehav.2012.07.027

Collier, K., Radford, A. N., Townsend, S. W., & Manser, M. B. (2017). Wild dwarf mongooses produce general alert and predator-specific alarm calls. *Behavioral Ecology, 28,* 1293–1301. http://dx.doi.org/10.1093/beheco/arx091

Crockford, C., & Boesch, C. (2005). Call combinations in wild chimpanzees. *Behaviour, 142,* 397–421. http://dx.doi.org/10.1163/1568539054012047

Croft, D. P., Edenbrow, M., Darden, S. K., Ramnarine, I. W., van Oosterhout, C., & Cable, J. (2011). Effect of gyrodactylid ectoparasites on host behaviour and social network structure in guppies Poecilia reticulata. *Behavioral Ecology and Sociobiology, 65,* 2219–2227. http://dx.doi.org/10.1007/s00265-011-1230-2

Croft, D. P., James, R., & Krause, J. (2008). *Exploring animal social networks*. Princeton, NJ: Princeton University Press. http://dx.doi.org/10.1515/9781400837762

Cronin, K. A. (2012). Prosocial behaviour in animals: The influence of social relationships, communication and rewards. *Animal Behaviour, 84,* 1085–1093. http://dx.doi.org/10.1016/j.anbehav.2012.08.009

DeCasien, A. R., Williams, S. A., Higham, J. P. (2017). Primate brain size is predicted by diet but not sociality. *Nature Ecology and Evolution, 1,* 0112. http://dx.doi.org/10.1038/s41559-017-0112

de Waal, F. B. M., & Tyack, P. L. (2003). *Animal social complexity: Intelligence, culture, and individualized societies*. Cambridge, MA: Harvard University Press. http://dx.doi.org/10.4159/harvard.9780674419131

Dobson, S. D. (2009). Socioecological correlates of facial mobility in nonhuman anthropoids. *American Journal of Physical Anthropology, 139,* 413–420. http://dx.doi.org/10.1002/ajpa.21007

Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology, 6,* 178–190. http://dx.doi.org/10.1002/(SICI)1520-6505(1998)6:5<178::AID-EVAN5>3.0.CO;2-8

Dunbar, R. I. M. (2003). The social brain: Mind, language, and society in evolutionary perspective. *Annual Review of Anthropology, 32,* 163–181. http://dx.doi.org/10.1146/annurev.anthro.32.061002.093158

Dunbar, R. I. M. (2009). The social brain hypothesis and its implications for social evolution. *Annals of Human Biology, 36,* 562–572. http://dx.doi.org/10.1080/03014460902960289

Dunbar, R. I. M., & Shultz, S. (2017). Why are there so many explanations for primate brain evolution? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 372,* 20160244. http://dx.doi.org/10.1098/rstb.2016.0244

Easley, D., & Kleinberg, J. (2010). *Networks, crowds, and markets: Reasoning about a highly connected world*. Cambridge, NY: Cambridge University Press. http://dx.doi.org/10.1017/CBO9780511761942

Engesser, S., Ridley, A. R., & Townsend, S. W. (2016). Meaningful call combinations and compositional processing in the southern pied babbler. *Proceedings of the National Academy of Sciences of the United States of America, 113,* 5976–5981. http://dx.doi.org/10.1073/pnas.1600970113

Engesser, S., Ridley, A. R., & Townsend, S. W. (2017). Element repetition rates encode functionally distinct information in pied babbler ‘clucks’ and ‘purrs’. *Animal Cognition, 20,* 953–960. http://dx.doi.org/10.1007/s10071-017-1114-6

Fedurek, P., Donnellan, E., & Slocombe, K. E. (2014). Social and ecological correlates of long-distance pant hoot calls in male chimpanzees. *Behavioral Ecology and Sociobiology, 68,* 1345–1355. http://dx.doi.org/10.1007/s00265-014-1745-4

Fedurek, P., Zuberbühler, K., & Dahl, C. D. (2016). Sequential information in a great ape utterance. *Scientific Reports, 6,* 38226. http://dx.doi.org/10.1038/srep38226

Ficken, M. S. (1990). Acoustic characteristics of alarm calls associated with predation risk in chickadees. *Animal Behaviour, 39,* 400–401. http://dx.doi.org/10.1016/S0003-3472(05)80888-7

Fischer, J., Farnworth, M. S., Sennhenn-Reulen, H., & Hammerschmidt, K. (2017). Quantifying social complexity. *Animal Behaviour, 130,* 57–66. http://dx.doi.org/10.1016/j.anbehav.2017.06.003

Flower, T. (2011). Fork-tailed drongos use deceptive mimicked alarm calls to steal food. *Proceedings of the Royal Society B: Biological Sciences, 278,* 1548–1555. http://dx.doi.org/10.1098/rspb.2010.1932

Foster, S. A., & Endler, J. A. (1999). *Geographic variation in behavior: Perspectives on evolutionary mechanisms*. New York, NY: Oxford University Press.

Freeberg, T. M., Dunbar, R. I. M., & Ord, T. J. (2012). Social complexity as a proximate and ultimate factor in communicative complexity. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences, 367,* 1785–1801. http://dx.doi.org/10.1098/rstb.2011.0213

Freeberg, T. M., Eppert, S. K., Sieving, K. E., Lucas, J. R. (2017). Diversity in mixed species groups improves success in a novel feeder test in a wild songbird community. *Scientific Reports, 7,* 43014. http://dx.doi.org/10.1038/srep43014

Freeberg, T. M., & Krams, I. (2015). Does social complexity link vocal complexity and cooperation? *Journal of Ornithology, 156,* 125–132. http://dx.doi.org/10.1007/s10336-015-1233-2

Freeberg, T. M., & Lucas, J. R. (2012). Information theoretical approaches to chick-a-dee calls of Carolina chickadees (*Poecile carolinensis*). *Journal of Comparative Psychology, 126,* 68–81. http://dx.doi.org/10.1037/a0024906

Freeberg, T. M., Lucas, J. R., & Clucas, B. (2003). Variation in chick-a-dee calls of a Carolina chickadee population, Poecile carolinensis: Identity and redundancy within note types. *The Journal of the Acoustical Society of America, 113,* 2127–2136. http://dx.doi.org/10.1121/1.1559175

Gordon, D. M. (2010). *Ant encounters: Interaction networks and colony behavior*. Princeton, NJ: Princeton University Press. http://dx.doi.org/10.1515/9781400835447

Graham, K. E., Furuichi, T., & Byrne, R. W. (2017). The gestural repertoire of the wild bonobo (*Pan paniscus*): A mutually understood communication system. *Animal Cognition, 20,* 171–177. http://dx.doi.org/10.1007/s10071-016-1035-9

Harrison, D. A., & Klein, K. J. (2007). What’s the difference? Diversity constructs as separation, variety, or disparity in organizations. *The Academy of Management Review, 32,* 1199–1228. http://dx.doi.org/10.5465/amr.2007.26586096

Healy, S. D., & Rowe, C. (2007). A critique of comparative studies of brain size. *Proceedings of the Royal Society B: Biological Sciences, 274,* 453–464. http://dx.doi.org/10.1098/rspb.2006.3748

Healy, S. D., & Rowe, C. (2013). Costs and benefits of evolving a larger brain: Doubts over the evidence that large brains lead to better cognition. *Animal Behaviour, 86,* e1–e3. http://dx.doi.org/10.1016/j.anbehav.2013.05.017

Henry, K. S., Gall, M. D., Velez, A., & Lucas, J. R. (2016). Avian auditory processing at four different scales: Variation among species, seasons, sexes, and individuals. In M. A. Bee & C. T. Miller (Eds.), *Psychological mechanisms in animal communication* (pp. 17–55). Cham, Switzerland: Springer International Publishing. http://dx.doi.org/10.1007/978-3-319-48690-1_2

Henry, K. S., & Lucas, J. R. (2008). Coevolution of auditory sensitivity and temporal resolution with acoustic signal space in three songbirds. *Animal Behaviour, 76,* 1659–1671. http://dx.doi.org/10.1016/j.anbehav.2008.08.003

Hobaiter, C., Byrne, R. W., & Zuberbühler, K. (2017). Wild chimpanzees’ use of single and combined vocal and gestural signals. *Behavioral Ecology and Sociobiology, 71,* 96–108. http://dx.doi.org/10.1007/s00265-017-2325-1

Hobaiter, C., Leavens, D. A., & Byrne, R. W. (2014). Deictic gesturing in wild chimpanzees (*Pan troglodytes*)? Some possible cases. *Journal of*

Comparative Psychology, 128, 82–87. http://dx.doi.org/10.1037/a0033757

Holekamp, K. E., Dantzer, B., Stricker, G., Shaw Yoshida, K. C., & Benson-Amram, S. (2015). Brains, brawn and sociality: A hyaena's tale. *Animal Behaviour, 103,* 237–248. http://dx.doi.org/10.1016/j.anbehav.2015.01.023

Humphrey, N. K. (1976). The social function of intellect. In P. P. G. Bateson & R. A. Hinde (Eds.), *Growing points in ethology* (pp. 303–317). Cambridge, NY: Cambridge University Press.

Jolly, A. (1966). Lemur social behavior and primate intelligence. *Science, 153,* 501–506. http://dx.doi.org/10.1126/science.153.3735.501

Kasper, C., & Voelkl, B. (2009). A social network analysis of primate groups. *Primates, 50,* 343–356. http://dx.doi.org/10.1007/s10329-009-0153-2

Kean, D., Tiddi, B., Fahy, M., Heistermann, M., Schino, G., & Wheeler, B. C. (2017). Feeling anxious? The mechanisms of vocal deception in tufted capuchin monkeys. *Animal Behaviour, 130,* 37–46. http://dx.doi.org/10.1016/j.anbehav.2017.06.008

Kern, J. M., Laker, P. R., & Radford, A. N. (2017). Contextual variation in the alarm call responses of dwarf mongooses, Helogale parvula. *Animal Behaviour, 127,* 43–51. http://dx.doi.org/10.1016/j.anbehav.2017.03.002

Kershenbaum, A. (2014). Entropy rate as a measure of animal vocal complexity. *Bioacoustics: The International Journal of Animal Sound and Its Recording, 23,* 195–208. http://dx.doi.org/10.1080/09524622.2013.850040

Kershenbaum, A., & Blumstein, D. T. (2017). Introduction to the special column: Communication, cooperation, and cognition in predators. *Current Zoology, 63,* 295–299. http://dx.doi.org/10.1093/cz/zox027

Kershenbaum, A., Blumstein, D. T., Roch, M. A., AKçay, Ç., Backus, G., Bee, M. A., . . . Zamora-Gutierrez, V. (2016). Acoustic sequences in non-human animals: A tutorial review and prospectus. *Biological Reviews of the Cambridge Philosophical Society, 91,* 13–52. http://dx.doi.org/10.1111/brv.12160

Kotrschal, A., Rogell, B., Bundsen, A., Svensson, B., Zajitschek, S., Brännström, I., . . . Kolm, N. (2013). Artificial selection on relative brain size in the guppy reveals costs and benefits of evolving a larger brain. *Current Biology, 23,* 168–171. http://dx.doi.org/10.1016/j.cub.2012.11.058

Krama, T., Vrublevska, J., Freeberg, T. M., Kullberg, C., Rantala, M. J., & Krams, I. (2012). You mob my owl, I'll mob yours: Birds play tit-for-tat game. *Scientific Reports, 2,* 800. http://dx.doi.org/10.1038/srep00800

Krams, I., Krama, T., Freeberg, T. M., Kullberg, C., & Lucas, J. R. (2012). Linking social complexity and vocal complexity: A parid perspective. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences, 367,* 1879–1891. http://dx.doi.org/10.1098/rstb.2011.0222

Krause, J., James, R., Franks, D., & Croft, D. (2015). *Animal social networks*. Oxford, United Kingdom: Oxford University Press.

Krause, S., James, R., Faria, J. J., Ruxton, G. D., & Krause, J. (2011). Swarm intelligence in humans: Diversity can trump ability. *Animal Behaviour, 81,* 941–948. http://dx.doi.org/10.1016/j.anbehav.2010.12.018

Kulahci, I. G., Rubenstein, D. I., Bugnyar, T., Hoppitt, W., Mikus, N., & Schwab, C. (2016). Social networks predict selective observation and information spread in ravens. *Royal Society Open Science, 3,* 160256. http://dx.doi.org/10.1098/rsos.160256

Kulahci, I. G., Rubenstein, D. I., & Ghazanfar, A. A. (2015). Lemurs groom-at-a-distance through vocal networks. *Animal Behaviour, 110,* 179–186. http://dx.doi.org/10.1016/j.anbehav.2015.09.016

Lengagne, T., Aubin, T., Lauga, J., & Jouventin, P. (1999). How do king penguins (*Aptenodytes patagonicus*) apply the mathematical theory of information to communicate in windy conditions? *Proceedings of the Royal Society B: Biological Sciences, 266,* 1623–1628. http://dx.doi.org/10.1098/rspb.1999.0824

Leonhardt, S. D., Menzel, F., Nehring, V., & Schmitt, T. (2016). Ecology and evolution of communication in social insects. *Cell, 164,* 1277–1287. http://dx.doi.org/10.1016/j.cell.2016.01.035

Liebal, K., Waller, B. M., Burrows, A. M., & Slocombe, K. E. (2014). *Primate communication: A multimodal approach*. New York, NY: Cambridge University Press.

Lusseau, D. (2003). The emergent properties of a dolphin social network. *Proceedings of the Royal Society B: Biological Sciences, 270*(Suppl. 2), S186–S188. http://dx.doi.org/10.1098/rsbl.2003.0057

MacLean, E. L., Barrickman, N. L., Johnson, E. M., & Wall, C. E. (2009). Sociality, ecology, and relative brain size in lemurs. *Journal of Human Evolution, 56,* 471–478. http://dx.doi.org/10.1016/j.jhevol.2008.12.005

Maestripieri, D. (2005). Gestural communication in three species of macaques (*Macaca mulatta, M. nemestrina, M. arctoides*): Use of signals in relation to dominance and social context. *Gesture, 5,* 57–73. http://dx.doi.org/10.1075/gest.5.1.06mae

Marino, L. (2017). Thinking chickens: A review of cognition, emotion, and behavior in the domestic chicken. *Animal Cognition, 20,* 127–147. http://dx.doi.org/10.1007/s10071-016-1064-4

Marler, P., Dufty, A., & Pickert, R. (1986). Vocal communication in the domestic chicken: 1. Does a sender communicate information about the quality of a food referent to a receiver. *Animal Behaviour, 34,* 188–193. http://dx.doi.org/10.1016/0003-3472(86)90022-9

Maynard Smith, J., & Harper, D. (2003). *Animal Signals*. Oxford, United Kingdom: Oxford University Press.

McShea, D. W. (1996). Perspective Metazoan complexity and evolution: Is there a trend? *Evolution; International Journal of Organic Evolution, 50,* 477–492.

McShea, D. W. (2005). The evolution of complexity without natural selection, a possible large-scale trend of the fourth kind. *Paleobiology, 31,* 146–156. http://dx.doi.org/10.1666/0094-8373(2005)031[0146:TEOCWN]2.0.CO;2

McShea, D. W., & Brandon, R. N. (2010). *Biology's first law: The tendency for diversity and complexity to increase in evolutionary systems*. Chicago, IL: University of Chicago Press. http://dx.doi.org/10.7208/chicago/9780226562278.001.0001

Meadows, D. H. (2008). *Thinking in systems: A primer*. D. Wright (Ed.). London, United Kingdom: Sustainability Institute/Earthscan.

Mokkonen, M., & Lindstedt, C. (2016). The evolutionary ecology of deception. *Biological Reviews of the Cambridge Philosophical Society, 91,* 1020–1035. http://dx.doi.org/10.1111/brv.12208

Morand-Ferron, J., & Quinn, J. L. (2011). Larger groups of passerines are more efficient problem solvers in the wild. *Proceedings of the National Academy of Sciences of the United States of America, 108,* 15898–15903. http://dx.doi.org/10.1073/pnas.1111560108

Morton, E. S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist, 111,* 855–869. http://dx.doi.org/10.1086/283219

Mowles, S. L., Jennions, M., & Backwell, P. R. Y. (2017). Multimodal communication in courting fiddler crabs reveals male performance capacities. *Royal Society Open Science, 4,* 161093. http://dx.doi.org/10.1098/rsos.161093

Nelson, D. A., & Marler, P. (1990). The perception of birdsong and an ecological concept of signal space. In W. C. Stebbins, & M. A. Berkley (Eds.), *Comparative perception. Vol II. Complex signals* (pp. 443–478). New York, NY: Wiley.

Nuechterlein, G. L., & Buitron, D. (2006). Advertising by western grebes: Bout-length variability and signal confusion in a multiple-use call. *Behaviour, 143,* 1547–1562. http://dx.doi.org/10.1163/156853906779367008

Ord, T. J., Blumstein, D. T., & Evans, C. S. (2002). Ecology and signal evolution in lizards. *Biological Journal of the Linnean Society Linnean Society of London, 77,* 127–148. http://dx.doi.org/10.1046/j.1095-8312.2002.00100.x

Ouattara, K., Lemasson, A., & Zuberbühler, K. (2009). Campbell's monkeys concatenate vocalizations into context-specific call sequences. *Proceedings of the National Academy of Sciences of the United States of America, 106,* 22026–22031. http://dx.doi.org/10.1073/pnas.0908118106

Owings, D. H., & Morton, E. S. (1998). *Animal vocal communication: A new approach*. Cambridge, United Kingdom: Cambridge University Press. http://dx.doi.org/10.1017/CBO9781139167901

Page, S. E. (2011). *Diversity and complexity*. Princeton, NJ: Princeton University Press.

Partan, S., & Marler, P. (1999). Communication goes multimodal. *Science, 283,* 1272–1273. http://dx.doi.org/10.1126/science.283.5406.1272

Pasquaretta, C., Levé, M., Claidière, N., van de Waal, E., Whiten, A., MacIntosh, A. J. J., . . . Sueur, C. (2015). Social networks in primates: Smart and tolerant species have more efficient networks. *Scientific Reports, 4,* 7600. http://dx.doi.org/10.1038/srep07600

Pérez-Barbería, F. J., Shultz, S., & Dunbar, R. I. M. (2007). Evidence for coevolution of sociality and relative brain size in three orders of mammals. *Evolution: International Journal of Organic Evolution, 61,* 2811–2821. http://dx.doi.org/10.1111/j.1558-5646.2007.00229.x

Pollard, K. A., & Blumstein, D. T. (2012). Evolving communicative complexity: Insights from rodents and beyond. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences, 367,* 1869–1878. http://dx.doi.org/10.1098/rstb.2011.0221

Powell, L. E., Isler, K., & Barton, R. A. (2017). Re-evaluating the link between brain size and behavioural ecology in primates. *Proceedings of the Royal Society B: Biological Sciences, 284,* 20171765. http://dx.doi.org/10.1098/rspb.2017.1765

Price, J. J. (1999). Recognition of family-specific calls in stripe-backed wrens. *Animal Behaviour, 57,* 483–492. http://dx.doi.org/10.1006/anbe.1998.1018

Puga-Gonzalez, I., & Sueur, C. (2017). Emergence of complex social networks from spatial structure and rules of thumb: A modelling approach. *Ecological Complexity, 31,* 189–200. http://dx.doi.org/10.1016/j.ecocom.2017.07.004

Reader, S. M., Morand-Ferron, J., & Flynn, E. (2016). Animal and human innovation: Novel problems and novel solutions. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 371,* 20150182. http://dx.doi.org/10.1098/rstb.2015.0182

Rendall, D., Owren, M. J., & Ryan, M. J. (2009). What do animal signals mean? *Animal Behaviour, 78,* 233–240. http://dx.doi.org/10.1016/j.anbehav.2009.06.007

Roberts, A. I., Vick, S.-J., & Buchanan-Smith, H. M. (2013). Communicative intentions in wild chimpanzees: Persistence and elaboration in gestural signalling. *Animal Cognition, 16,* 187–196. http://dx.doi.org/10.1007/s10071-012-0563-1

Roberts, S. G. B., & Roberts, A. I. (2016). Social brain hypothesis: Vocal and gesture networks of wild chimpanzees. *Frontiers in Psychology, 7,* 1756. http://dx.doi.org/10.3389/fpsyg.2016.01756

Ronald, K. L., Fernandez-Juricic, E., & Lucas, J. R. (2012). Taking the sensory approach: How individual differences in sensory perception can influence mate choice. *Animal Behaviour, 84,* 1283–1294. http://dx.doi.org/10.1016/j.anbehav.2012.09.015

Ronald, K. L., Zeng, R., White, D., Fernandez-Juricic, E., & Lucas, J. R. (2017). What makes a multimodal signal attractive? A preference function approach. *Behavioral Ecology, 28,* 677–687. http://dx.doi.org/10.1093/beheco/arx015

Ryan, M. J., & Cummings, M. E. (2013). Perceptual biases and mate choice. *Annual Review of Ecology Evolution and Systematics, 44,* 437–459. http://dx.doi.org/10.1146/annurev-ecolsys-110512-135901

Sallet, J., Mars, R. B., Noonan, M. P., Andersson, J. L., O'Reilly, J. X., Jbabdi, S., . . . Rushworth, M. F. (2011). Social network size affects neural circuits in macaques. *Science, 334,* 697–700. http://dx.doi.org/10.1126/science.1210027

Schel, A. M., Machanda, Z., Townsend, S. W., Zuberbühler, K., & Slocombe, K. E. (2013). Chimpanzee food calls are directed at specific individuals. *Animal Behaviour, 86,* 955–965. http://dx.doi.org/10.1016/j.anbehav.2013.08.013

Scott, J. (2012). *Social network analysis: A handbook* (3rd ed.). London, United Kingdom: Sage.

Sewall, K. B. (2015). Social complexity as a driver of communication and cognition. *Integrative and Comparative Biology, 55,* 384–395. http://dx.doi.org/10.1093/icb/icv064

Seyfarth, R. M., & Cheney, D. L. (2015). Social cognition. *Animal Behaviour, 103,* 191–202. http://dx.doi.org/10.1016/j.anbehav.2015.01.030

Seyfarth, R. M., Cheney, D. L., Bergman, T., Fischer, J., Zuberbühler, K., & Hammerschmidt, K. (2010). The central importance of information in studies of animal communication. *Animal Behaviour, 80,* 3–8. http://dx.doi.org/10.1016/j.anbehav.2010.04.012

Shannon, C. E., & Weaver, W. (1949). *The mathematical theory of communication*. Urbana: University of Illinois Press.

Shettleworth, S. J. (2010). *Cognition, evolution, and behavior* (2nd ed.). New York, NY: Oxford University Press.

Shultz, S., & Dunbar, R. I. M. (2007). The evolution of the social brain: Anthropoid primates contrast with other vertebrates. *Proceedings of the Royal Society B: Biological Sciences, 274,* 2429–2436. http://dx.doi.org/10.1098/rspb.2007.0693

Slobodchikoff, C. N., & Placer, J. (2006). Acoustic structures in the alarm calls of Gunnison's prairie dogs. *The Journal of the Acoustical Society of America, 119,* 3153–3160. http://dx.doi.org/10.1121/1.2185489

Slocombe, K. E., & Zuberbühler, K. (2006). Food-associated calls in chimpanzees: Responses to food types or food preferences? *Animal Behaviour, 72,* 989–999. http://dx.doi.org/10.1016/j.anbehav.2006.01.030

Snijders, L., & Naguib, M. (2017). Communication in animal social networks: A missing link? In M. Naguib, J. Podos, L. W. Simmons, L. Barrett, S. D. Healy, & M. Zuk (Eds.), *Advances in the Study of Behavior* (Vol. 49, pp. 297–359). San Diego, CA: Elsevier Academic Press Inc. http://dx.doi.org/10.1016/bs.asb.2017.02.004

Stegmann, U. E. (Ed.), (2013). *Animal communication theory: Information and influence*. Cambridge, United Kingdom: Cambridge University Press. http://dx.doi.org/10.1017/CBO9781139003551

Street, S. E., Navarrete, A. F., Reader, S. M., & Laland, K. N. (2017). Coevolution of cultural intelligence, extended life history, sociality, and brain size in primates. *Proceedings of the National Academy of Sciences of the United States of America, 114,* 7908–7914. http://dx.doi.org/10.1073/pnas.1620734114

Suzuki, T. N., Wheatcroft, D., & Griesser, M. (2016). Experimental evidence for compositional syntax in bird calls. *Nature Communications, 7,* 10986. http://dx.doi.org/10.1038/ncomms10986

Tibbetts, E. A. (2004). Complex social behaviour can select for variability in visual features: A case study in *Polistes* wasps. *Proceedings of the Royal Society B: Biological Sciences, 271,* 1955–1960. http://dx.doi.org/10.1098/rspb.2004.2784

Tyack, P. L. (2008). Convergence of calls as animals form social bonds, active compensation for noisy communication channels, and the evolution of vocal learning in mammals. *Journal of Comparative Psychology, 122,* 319–331. http://dx.doi.org/10.1037/a0013087

Vanden Hole, C., Van Daele, A. A. G., Desmet, N., Devos, P., & Adriaens, D. (2014). Does sociality imply a complex vocal communication system? A case study for *Fukomys micklemi* (Bathyergidae, Rodentia). *Bioacoustics-the International Journal of Animal Sound and Its Recording, 23,* 143–160.

van Schaik, C. P., Isler, K., & Burkart, J. M. (2012). Explaining brain size variation: From social to cultural brain. *Trends in Cognitive Sciences, 16,* 277–284. http://dx.doi.org/10.1016/j.tics.2012.04.004

Voelkl, B., & Noe, R. (2010). Simulation of information propagation in real-life primate networks: Longevity, fecundity, fidelity. *Behavioral*

Ecology and Sociobiology, 64, 1449–1459. http://dx.doi.org/10.1007/s00265-010-0960-x

Vonk, J. (2016). Bigger brains may make better problem-solving carnivores. *Learning and Behavior, 44,* 99–100. http://dx.doi.org/10.3758/s13420-016-0222-5

Walker, R., Burger, O., Wagner, J., & Von Rueden, C. R. (2006). Evolution of brain size and juvenile periods in primates. *Journal of Human Evolution, 51,* 480–489. http://dx.doi.org/10.1016/j.jhevol.2006.06.002

Weldon, P. J. (2017). Receiver-error in deception, including mimicry: Making the leap from inter- to intraspecific domains. *Biological Journal of the Linnean Society Linnean Society of London, 120,* 717–728.

West, R. J. D. (2014). The evolution of large brain size in birds is related to social, not genetic, monogamy. *Biological Journal of the Linnean Society Linnean Society of London, 111,* 668–678. http://dx.doi.org/10.1111/bij.12193

Wheeler, B. C. (2009). Monkeys crying wolf? Tufted capuchin monkeys use anti-predator calls to usurp resources from conspecifics. *Proceedings of the Royal Society B: Biological Sciences, 276,* 3013–3018. http://dx.doi.org/10.1098/rspb.2009.0544

Whiten, A. (2000). Social complexity and social intelligence. In G. R. Bock, J. A. Goode, & K. Webb (Eds.), *The nature of intelligence, Vol. Novartis Foundation Symposium 233* (pp. 185–201). Chichester, United Kingdom: Wiley.

Wilson, D. R., & Evans, C. S. (2008). Mating success increases alarm-calling effort in male fowl, *Gallus gallus*. *Animal Behaviour, 76,* 2029–2035. http://dx.doi.org/10.1016/j.anbehav.2008.08.021

Yurk, H., Barrett-Lennard, L., Ford, J. K. B., & Matkin, C. O. (2002). Cultural transmission within maternal lineages: Vocal clans in resident killer whales in southern Alaska. *Animal Behaviour, 63,* 1103–1119. http://dx.doi.org/10.1006/anbe.2002.3012

Zimmermann, E. (2017). Evolutionary origins of primate vocal communication: Diversity, flexibility, and complexity of vocalizations in basal primates. In R. M. Quam, M. A. Ramsier, R. R. Fay, & A. N. Popper (Eds.), *Primate hearing and communication* (Vol. 63, pp. 109–140). Cham, Switzerland: Springer International Publishing Ag. http://dx.doi.org/10.1007/978-3-319-59478-1_5

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