Title page

Communicative roots of complex sociality and cognition

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ABSTRACT

Mammals living in more complex social groups typically have large brains for their body size and many researchers have proposed that the primary driver of the increase in brain size through primate and hominin evolution are the selection pressures associated with sociality. Many mammals, and especially primates, use flexible signals that show a high degree of voluntary control and these signals may play an important role in maintaining and coordinating interactions between group members. However, the specific role that cognitive skills play in this complex communication, and how in turn this relates to sociality, is still unclear. The hypothesis for the communicative roots of complex sociality and cognition posits that in socially complex species, conspecifics develop and maintain bonded relationships through cognitively complex communication more effectively than through less cognitively complex communication. We review the research evidence in support of this hypothesis and how key features of complex communication such as intentionality and referentiality are underpinned by complex cognitive abilities. Exploring the link between cognition, communication and sociality provides insights into how increasing flexibility in communication can facilitate the emergence of social systems characterized by bonded social relationships, such as those found in primates and humans. To move the field forward and carry out both the within and between species comparisons, we advocate the use of social network analysis, which provides a novel way to describe and compare social structure. Using this approach can lead to a new, systematic way of examining social and communicative complexity across species, something that is lacking in current comparative studies of social structure.

KEYWORDS: Hypothesis for communicative roots of complex sociality and cognition, social bonding, social evolution, communicative complexity, primates, brain size, social network analysis

I. INTRODUCTION

One of the distinctive features of primates is that they have unusually large brains for their body size (Jerison, 1975). This observation has led to an active debate about the factors that selected for the evolution of large brains in primates (e.g. Barrickman, Bastian, Isler *et al.*, 2008; Barton, 1996; Byrne & Whiten, 1989; Clutton-Brock & Harvey, 1980; Dunbar, 1992; Dunbar, 1998; Evans, Gilbert, Mekel-Bobrov *et al.*, 2005; Finlay, Darlington & Nicastro, 2001; Gibson, 1986; Harvey, Clutton-Brock & Mace, 1980; Hofman, 1983; MacLean, Hare, Nunn *et al.*, 2014; Miller, 1999; Moll & Tomasello, 2007; Reader & Laland, 2002; Van Schaik, Isler & Burkart, 2012). The comparative method has been exploited as a powerful tool that has enabled scientists to increase our understanding of how the pressures of the socio-ecological environment have influenced the variation in brain size across primate species.

Social explanations have centred on the role of sociality in explaining brain size evolution. Early studies suggested that behavioural innovation and social transmission of behaviour (or generally information) explain relative brain size variation in non-human primates, because they are cognitively demanding as they require that individuals flexibly learn from others and invent new behaviours. This cognitive capacity enables primates to exploit their environment in new ways and so expose them to advantages of novel selection pressures (Lefebvre, Whittle, Lascaris *et al.*, 1997; Reader, Hager & Laland, 2011; Reader & Laland, 2002; Van Schaik *et al.*, 2012; Wyles, Kunkel & Wilson, 1983). Using ecologically relevant measures of cognitive ability such as relative and absolute "executive" brain volumes, an influential study showed that the incidence of behavioural innovation, social learning, and tool use correlate with brain size and cognitive capacities of primates (Reader & Laland, 2002). Another proposal that has received considerable research attention is the social intelligence hypothesis. This hypothesis also regarded behavioural flexibility as a key factor driving evolution of large brains in primates (Byrne & Whiten, 1989; Reader & Laland, 2002; Whiten & Byrne, 1997). Arguing that primate social environments are inherently competitive, the nature of social environment would lead to a selection pressure for the evolution of "Machiavellian" strategies. Using tactical deception as a defining criterion for this hypothesis, Byrne and Corp (2004) showed how the frequency of tactical deception correlates with neocortex volume in primates, suggesting that strategies of social manoeuvring have driven evolution of larger brains in socially complex species.

These social explanations have been opposed by ecological hypotheses, suggesting that the enlarged brains and generally complex cognitive skills in primates may be explained by ecological factors (Powell, Isler & Barton, 2017) such as "extractive foraging" (Parker & Gibson, 1977) and "cognitive mapping" (Milton, 1988). Mentally tracking and finding the location of scattered and unpredictable foods is cognitively demanding and therefore primate species exhibiting greater dietary complexity are hypothesized to have larger brains than species exhibiting lower dietary complexity (DeCasien, Williams & Higham, 2017; MacLean *et al.*, 2014). Fruit is more scattered and unpredictable than folivorous foods. Thus, early studies proposed that primates with more complex frugivorous diets have larger brains than folivorous species. However, phylogenetic comparative analyses initially found no link between the degree of dietary frugivory and brain size when controlling for social group size across mammals (Navarrete, van Schaik & Isler, 2011; Silva & Downing, 1995; Wrangham & Carmody, 2010). However, new evidence using a larger sample of primates, more recent phylogenies, and updated statistical techniques, showed that brain size is predicted by diet, rather than multiple measures of sociality, after controlling for body size and phylogeny (DeCasien *et al.*, 2017). For instance, frugivorous lemur species have more sophisticated cognitive skills (inhibitory control, memory) than folivorous lemur species. This new evidence has reignited the debate over which factors - social or ecological - are of key importance in primate brain size evolution.

What is generally agreed upon, even if this still needs to be debated, is that anthropoid social evolution is generally characterised by a relationship between the level of encephalization and the complexity of social system (Broad, Curley & Keverne, 2006; Curley & Keverne, 2005). The highest rates of encephalisation can be found in the Primates but also other mammalian families such as Hippomorphs (horse family), Tylopods (camel family), the Odontocetes (dolphin family) and the Caniniformes (dog family) (Dunbar & Shultz, 2010). However, among mammalian species, the anthropoid primates stand out as having a particularly strong correlation between the complexity of the social system (typically quantified as group size) and brain size, and specifically the neocortex size in relation to the rest of the brain (the neocortex ratio). Thus in many non-primate species, a pairbonded mating system rather than group size is associated with larger brain size (Shultz & Dunbar, 2007). In contrast, in primates there is a strong relationship between group size and brain size. This empirical finding has been taken to support the hypothesis that the demands of maintaining stable social bonds within social groups are particularly important in explaining encephalization in primate species as compared to other mammals (Broad *et al.*, 2006; Shultz & Dunbar, 2007). However, there is a lack of studies examining how this social complexity would function at a behavioural level i.e. in the interactions between a specific pair of animals, and at the cognitive level, in terms of the cognitive processes involved in these interactions and in managing these relationships. This makes it unclear exactly what would make primate sociality more ‘cognitively complex’ than other mammalian species (Dunbar & Shultz, 2010).

Group size is limited both by the time demands of maintaining social relationships (Dunbar & Shultz, 2017) and by the cognitive demands arising from processing information about social relationships, which sets an upper limit on the number of social relationships that primates can keep track of (Dunbar, 1998). Group size is a correlate for social complexity, if only because the number of dyads and triads of social relationships that have to be socially managed increases as a power function of the number of individuals in a group. However, the social brain hypothesis is specifically about the selection pressures arising from the need to create a functional, bonded social group, with sociality driven by the need to solve the ecological challenge of predation (Dunbar & Shultz, 2007). Group size is an emergent property of primates' ability to maintain and coordinate social relationships and is used as an indicator of the complexity of social groups as it is one of the only few metrics available for a large number of primate species (Dunbar & Shultz, 2017). However, it is a relatively crude measure of social complexity, and does not provide a detailed explanation of why larger groups are more complex than smaller ones, or how the way in which the group is structured affects the number and types of relationships an individual primate has to keep track of. Further, there is little understanding of what it is about sociality and managing social relationships that is so demanding of neural computational power. Thus, studies linking social complexity and cognition should consider the relationship between managing a more complex network of relationships and neocortex size, not simply the quantitative relationship between group size and brain size. The attempts to date to quantify social complexity have focused on the more sophisticated social strategies that may characterize more complex social systems (Dunbar & Shultz, 2017). Primates with larger neocortices have higher rates of social play, more complex male mating strategies, higher levels of tactical deception, are more likely to form coalitions and have a higher frequency of social learning (Dunbar & Shultz, 2017). Although these theoretical approaches to social complexity are valuable to improving our understanding of the link between social complexity and cognition, they cannot provide a detailed explanation as to why primates are unusually encephalized as compared to other mammalian species, or why the relationship between encephalization and group size is stronger in primates than other mammalian species (Shultz & Dunbar, 2007).

To understand the link between social complexity and cognition, a detailed understanding of how primates interact with others to build and maintain social relationships over time is required, as this is at the heart of what makes primate life socially complex (Hinde, 1976). Many mammals (e.g. ungulates such as wildebeest) live in social groups but these groups are just loose aggregations, without stable membership or relationships between individuals. In contrast, primates live in groups with stable membership, where they form long-lasting and differentiated bonds outside of mating contexts. The quality of these bonds has important fitness consequences - for example, the sociality of adult female baboons is positively linked to infant survival (Silk, 2007).

The loose aggregations of many mammal species are believed to be a direct response to high costs of competition over resources such as food and mates (Dunbar & Shultz, 2010). In contrast, it has been proposed that primates evolved strategies of social bonding to buffer themselves against the inevitable stresses of group living such as feeding and mating competition (Dunbar & Shultz, 2017; Keverne, Martensz & Tuite, 1989). Perhaps the most potent strategy employed by primates is engaging in unidirectional grooming (one animal grooming another but not vice versa) as this releases endorphins, reducing stress in the recipient. As a consequence of unidirectional grooming, dyad partners increase their willingness to engage in social bonding behaviour. Although there is an inherent difficulty in defining what a social bond is in non-verbal animals, given it is experienced (or felt), a number of recent studies have defined bondedness in terms of behavioural criteria such as grooming reciprocity and responsiveness, mutual grooming, mutual visual contact, proximity to nearest neighbour and joint travel (Dunbar & Shultz, 2010). In order to build these social bonds, primates use communication to coordinate the grooming bouts that form the basis for stable social bond formation (Dunbar, 2010; Fedurek, Slocombe, Hartel *et al.*, 2015). Furthermore, primates use communication to build social ties with group members directly through rewarding function without unidirectional grooming (Fedurek, Machanda, Schel *et al.*, 2013; Roberts & Roberts, 2016b). Thus, communication is a crucial way of coordinating and regulating social relationships in primate societies, but the role of cognitive skills underpinning this communication in social bonding has received limited attention, despite its potential significance for furthering our understanding of how complexity of cognitive skills is related to complexity of sociality. Communication is defined as a use of gestures (non-verbal signals such as voluntary movements of the limbs or head and body postures, transmitted through visual, tactile or auditory channels), vocalisations (sounds made with the vocal tract) or facial expressions (motions of the muscles beneath the skin of the face), which appear to influence the receivers (Wilczynski & Ryan, 1999). Many acts might be less cognitively complex because they are involuntary reactions to the signaller's internal emotional state. In contrast, cognitively complex communication employs signals flexibly, which implies that signallers have voluntary control over communication (Tomasello & Zuberbühler, 2002).

The purpose of this piece is to explore the cognitive complexity in communication that may have led to the emergence of more complex social systems in primates. Here we strictly consider complex social systems as those where species form stable, bonded social relationships with unrelated individuals outside of mated pair (Dunbar & Shultz, 2017). The central idea behind this hypothesis is that in socially complex species, animals can form and maintain bonded social relationships in complex social settings through cognitively complex communication more effectively than through cognitively less complex communication (Roberts, Vick, Roberts *et al.*, 2014b). Thus, the evolution of cognitive skills underpinning communication in primates may have presented a key innovation that facilitated the emergence of more complex, bonded social systems which are not based on kinship or reproductive ties (Dunbar & Shultz, 2017; Roberts, Roberts & Vick, 2014a; Roberts, Vick, Roberts *et al.*, 2012b). In the Section 2 we discuss historical perspectives that precede this hypothesis. Section 3a sketches out communication innovations that may have enabled the kinds of bonded social relationships that we find in primates, Section 3b briefly examines how increases in complexity of communication may have enabled bonded relationships to emerge in more complex social systems of primates. In section 4 we briefly outline some of the empirical evidence from primate studies in support of the hypothesis. Finally, in sections 5 and 6 we describe how the study of communicative roots of socio-cognitive skills can be enhanced by use of social network analysis.

II. HISTRORICAL APPROACH

Jean-Baptise Lamarck and Charles Darwin were first pioneering figures to link size and complexity of social groups with communicative complexity. Making the first argument for the greater need for information transfer in socially complex societies, Lamarck wrote: 'The individuals . . . having largely increased their needs according as the societies which they formed became larger, had to multiply their ideas to an equivalent extent, and thus felt the need for communicating them to their fellows. We may imagine that this will have compelled them to increase and vary in the same degree the signs which they used for communicating these ideas . . . ' (Lamarck, 1809/1963 , p. 172). Following from this argument, Darwin insisted on the role of emotional expressions as a social bonding mechanism rather than communication functioning as a tool for information transfer. He argued that communication by means of the voice, gestures and expressions is of a great importance for maintaining social relationships in social animals. (Darwin, 1965, p. 60). In the twentieth century, Marler (1977, p.46) was amongst the strongest advocates of the link between social and communicative complexity, he noted: "the richest elaboration of systems of social communication should be expected in intraspecific relationships, especially where trends towards increasing interindividual cooperation converge with the emergence of social groupings consisting of close kin.". Elaborating on these ideas Waser (1982, p. 118) proposed that "the value to a signaler of broadcasting information to recipients, and thus the degree to which selection favors specialized 'information-transfer' abilities, depend[s] on the social system". In recent years, this debate was extended by Maestripieri (1999, p. 56). He suggested that an important avenue of research extending our understanding of the link between group size and brain size "would be to investigate whether there is a relationship between group size, encaphalization, and the size and complexity of the communicative repertoire across extant primate species". More recently, these ideas have been developed into the social complexity hypothesis for communication. According to this hypothesis, groups with complex social systems demand more complex communicative systems to manage interactions among group members (Blumstein & Armitage, 1997; Freeberg, Dunbar & Ord, 2012; Leighton, 2017; Marler & Mitani, 1988; Roberts and Roberts, 2016b;

Wilkinson, 2003). In complex societies, as compared with simpler societies, individuals interact frequently in many different contexts with many different individuals and also repeatedly interact with many of the same individuals in the social group over time (Freeberg *et al.*, 2012). Complex communication systems are defined as 'those that contain a large number of structurally and functionally distinct elements (e.g. large display repertoire sizes) or possess a high amount of bits of information' (p. 1787, Freeberg *et al.*, 2012). In the next section we build on these ideas and make a number of clear and testable predictions regarding the link between the complexity of cognitive skills underpinning communication and the complexity of sociality.

III. COMMUNICATIVE ROOTS OF COMPLEX SOCIALTY AND COGNITION

Two key mechanisms mediate the complexity of social systems in mammals. In the majority of small brained mammals (e.g. rodents), individual recognition and social affiliation are hormonally mediated through olfaction (Broad *et al.*, 2006). Olfactory inputs to areas of the brain concerned with social reward results in priming of social affiliation by hormones such as oxytocin (Keverne & Curley, 2004). Individuals form an 'olfactory memory', which promotes short-term selective affiliation towards the brood or a mate that is mainly necessary in the context of reproduction (Dluzen, Muraoka, Engelmann *et al.*, 2000). Mother-infant affiliation ceases after weaning and reproductive partners cease affiliation after mating, meaning that outside of the mother-infant and mating partner bonds, social relationships are characterised by high levels of antagonism (Broad *et al.*, 2006). In contrast, in large brained mammals such as primates and humans, social affiliation occurs even in the absence of olfactory input and priming by social hormones (Curley *et al.*, 2005). The olfactory inputs to the areas of the brain concerned with social reward are downregulated and replaced by neocortical inputs that promote 'emotional' reward through individual recognition of a partner by means of integration of information from multiple sources (e.g. sensory cues such as facial expression) (Schultz, Tremblay & Hollerman, 2000). The role of medial prefrontal cortex (mPFC) in this process also means that the emancipation of social affiliation from hormonal control is coupled with voluntary control over social bonding rather than involuntary stimulus response modes (Broad *et al.*, 2006).

Two key mechanisms of voluntary control over interactions feature heavily in explaining the patterns of social bonding in mammals. The first is the heavy emphasis on social bonding with kin (Hamilton, 1964). The second is the wealth of attention devoted to explaining the role of demographic constraints and conspecific similarity of features on social bonding. Thus, the inclusive fitness benefits of kinship, or the appeal of interacting with members of the same age cohort, are widely claimed to drive social bonding in primates. However, we do not have any convincing explanations of how primate societies emerge that are complex and large and whereby individuals routinely interact with conspecifics that are dissimilar and/or unrelated. We wish to argue that in order to explain the complexity of social systems in primates, we have to take into account both how the complexity of primate communication relates to patterns of social bonding and how the complexity of cognitive skills makes this communicative complexity possible (Roberts *et al.*, 2014b).

By definition, communication in any primate species has evolved to effectively influence the behaviour of the recipient. However, selection for effectiveness in communication may not always characterise social relationships in primates. If both the signaller and the recipient have a mutual interest in signalling and responding, then the signals will be simple because the signaller is sensitive to the fact that the recipient is likely to respond and the recipient is sensitive to the signals (Dawkins & Guilford, 1997). As a result, the lack of efficiency in communication has been noted in the use of low intensity communication that although adaptive in frequent one on one interactions due to lower stresses incurred by the interaction, may be ineffective at influencing behavioural change in the recipient when interests conflict (Nakayama, Goto, Kuraoka *et al.*, 2005; Roberts & Roberts, 2016a). In the next section we will outline a number of indices of cognitively complex communication that may increase the ability of the signaller to influence the behaviour of the recipient through lower intensity signals. A particularly important source of efficiency in low intensity signals comes from a whole range of characteristics affecting ability of the recipient to understand the goal of the signaller and respond adaptively. These include low intensity signals that are for example, structurally complex, intentional, referential, novel, and manually precise (e.g. right-handed). In circumstances when the communication takes place in complex social settings, which include other conspecifics than just signaller and the recipient dyad, this complexity can oppose reduced comprehension of low intensity signals, due to the distraction of monitoring the third party audience. A particularly important source of distraction comes from the presence of conspecifics who are more appealing social partners than the signaller. A whole range of behaviours are affected by the presence of a competitive audience and are responsible for making low intensity signals less effective carriers of information. These include joint attention and close proximity between signaller and the recipient, as well as the recipient's visual monitoring of the communication channel. The subsequent increases in complexity of low intensity signals to increase efficiency of signalling may initially enable social interactions in complex social setting. However, as the social complexity further increases, communication complexity may reach an asymptotic limit, at which even extreme increases in complexity of low intensity signals will have no bearing on the effectiveness of social interactions. As a result, the power of complex, low intensity signals to influence the recipient will decline and the social bond will weaken.

So far, one type of answer has been given to the question of how primates can influence the recipient when a low intensity but complex signal is clearly unsuccessful. Classical ethologists had been clear in proposing that one important way to make signals more effective in eliciting appropriate behaviour is by exaggeration of amplitude (Blute, 2006). For instance, the signaller might use a loud auditory vocalisation simply to get its message across, even if the signaller and receiver were separated by a short distance. Although this would open the way to increasing the efficiency of signals, on regular one on one basis this would lead to separation between partners, as the recipient avoids behaviour that is maladaptive (e.g. increasing their stress levels or anxiety on regular basis). A further, previously unexplored way in which signaller can influence the receiver is by increasing the reward value of communication. We will proceed to discuss in more detail in the next section how some signals have special properties that can stimulate the reward system of the recipient. Light, sweeping touch can stimulate the sense organs and reward centres in the brains of the recipient particularly strongly. Similarly, synchronized, high amplitude, rhythmical vocalisations appear to be particularly stimulating for group living primates. By making communication so appealing, signaller can redirect the recipient's attention from a competitive audience back onto themselves and increase the recipient's commitment to the social interaction. These rewarding features of communication can have a particularly powerful effect, such that the social cohesion of the group can be preserved in presence of social competition. The fact that a wide variety of socially complex primates and humans evolved these types of rewarding signals means that these signals are likely to have played particularly important role in social evolution.

Another, largely unexplored role of communication in animal societies is to facilitate recall of information in the recipient about the individual identity of the signaller. This role of communication has long been recognised in human studies, but only recently have primate studies suggested that communication accompanied by the use of directional communication such as mutual visual contact and pointing gestures made in the direction of the recipient, or distinctive communication such as unoverlapping repertoire signals made by the signaller towards the recipient, can increase the memory of the signaller to the recipient. This may act as a necessary prerequisite to establishing social bonding when social complexity increases.

From this it follows that socially complex primate species must solve problems relating to complexity of social world in which they live through cognitively complex communication. Primates must be able to flexibly adjust their communication according to the current situation. This cognitive flexibility is required to monitor and manage social relationships in a dynamic social environment. Primates must not only keep track of their own relationships, but also monitor third party relationships between other group members, as changes in these relationships (e.g. a change in dominance rank) can have implications for their own position in their group. There is a large body of evidence showing that primates have knowledge of third party relationships, in relation to, for example mother-infant relationships, relative dominance rankings and matrilines (Silk, 2007). In certain situations, it may be advantageous for primates to use knowledge about their own and third party relationships to adjust their communication according to which social partners are present or visually attending. This adjustment requires complex tracking of social relationships contingent on the memory of past interactions. Further, it demands an understanding of intentionality where to communicate effectively, the signaller has an understanding that the direct social relationship (that based on interaction between the signaller and the recipient) may differ from those relationships inferred from third-party interaction (that between the recipient and a third party audience) and that these third party relationships can affect the recipient's behaviour. This is equivalent to mentally modelling outcomes of different behavioural strategies that signallers can use towards the recipient and flexibly choosing one commination strategy over another to ensure this communication strategy is effective in influencing the recipient. Thus, emancipation from olfactory and hormonal determinants of affiliation would have been coupled with the increased importance of cognitively complex communication that is necessitated by living in a complex social group, in order to develop and maintain long lasting social bonds with unrelated group members. This illustrates the central point that we make in this paper that there is likely to be a need for increased cognitive complexity underpinning communication in socially complex primate species, compared with less socially complex species. Although there is good evidence of complex cognitive abilities underpinning communication in primates, we note that there is a relative scarcity of studies addressing ability of primates to maintain complex social relationships through the use of cognitively complex communication. To address this gap we first make a number of predictions about the types of cognitively complex communication in primates that should facilitate social bonding more effectively than cognitively simple communication (Fig. 1).

Second, we predict how enhanced cognitive complexity behind communication in primates may have resulted in increases in social complexity (Table 1).

a) Which features of primate communication facilitate social bonding?

(1) Complexity of structure

There is a large amount of variation observed in complexity of communication signals both across and within primate species. Communication signals can occur on their own, or they can be accompanied by the use of other signals, visual orientation or objects. Signals produced by the signaller can be homogenous and therefore occur in the repertoire of both the signaler and the recipient, or these signals can be heterogeneous, whereby signal occurs in the repertoire of the signaler but not in the repertoire of the recipient. Further, sequences of signals can have a varied composition, or contain repeated signals. In primates, a large complexity of signals is often interpreted as indicative of a greater underlying complexity of the cognitive skills involved in learning and flexibly producing this complex communication. One view is that complexity in communication is adaptive because it is more informative for the recipient than less complex signals and that in turn influences the efficiency with which the recipient can respond to communication (Dawkins and Guildord, 1997; Zahavi & Zahavi, 1997). For instance, facial expressions are processed independently in the amygdala giving rise to largely involuntary perceptions of another's communicative intent. However, combinations of facial expressions with directional cues (gaze direction and pointing gesture) are integrated in premotor cortex, enabling the recipient to more consciously evaluate the expectation of signaller's intent gained from processing of facial expression alone (Conty, Dezecache, Hugueville *et al.*, 2012). Thus, combinations of pointing gestures and gaze with facial expressions are more informative to the recipient than facial expressions alone and this enables the recipient to make more adaptive decisions about how to respond to communication. This indicates that complex communication would play an important role in regulating social interactions in complex social systems, whereby different types of signalling have different but complementary functions. There are however, many different ways in which signaller can achieve a greater efficiency of communication through encouraging complexity of signalling. The complexity of the structure in the form of discrete signals (with no intermediate forms between adjacent elements) or fluid signals that are not rigidly distinctive (signals that grade and change on a continuum from one prototypical form to another) (Marler, 1976) has also been linked to communicative and cognitive abilities (Roberts *et al.*, 2012b). In graded communication, the boundaries between the signal types are unclear and the signal types share many similar structural traits and components. The greater complexity of structure demands a greater degree of control by the signaller in the production of the precise form of communication. When the structure is flexible, primates create the structure of signals that they use, which may enable them to create more informative communication as compared to discrete signalling. As such greater complexity of communicative structure (i.e. graded repertoires) may be more common in socially complex species, as compared to less socially complex species.

(2) Perception

The ability to perceive communication is a critical aspect of social interactions (Seyfarth & Cheney, 2013). The overall structure of communication can influence processing of communication by the recipient because the complexity of structure is associated with the efficiency of communication processing. As the level of distinctiveness in repertoire increases, the association of the communication type with a specific goal or intention increases (Cottrell, Wack, Sekerak *et al.*, 1968; Zajonc & Sales, 1966). Thus, for the recipient, processing the content of a discrete signal and responding appropriately is relatively straightforward, as each signal is associated with a specific type of response. In contrast, for graded communication, a greater variety of signal types and forms are used in relation to specific goals or intentions (Roberts *et al.*, 2016a). Processing the content of graded signals and responding appropriately is a more cognitively complex task for the recipient and demands a greater degree of voluntary control underlying perception than discrete signals (Leavens, Hostetter, Wesley *et al.*, 2004; Pollick & de Waal, 2007). Given the greater processing demands of more complex communication, we would predict a greater capacity for decoding graded signals in species that live in complex social groups, as compared to those who live in less complex social groups.

(3) Intentionality

In intentional communication, the signaller has a goal and uses informative communication that refers to the role of the recipient in attaining the desired goal (Tomasello, George, Kruger *et al.*, 1985). For instance, the signaller indicates through the communication what the recipient should do and the recipient produces a response which matches the goal of the signaller as conveyed in the communication, enabling social behaviour to be coordinated (e.g. changing the behaviour from grooming to travel) (Golinkoff, 1986; Golinkoff, 1993). Such communication shows ability of the signaller to understand that the recipient is an intentional being with a goal state which may differ from one's own, but which can be altered by communicative behaviour (Tomasello, Hare & Fogleman, 2001). Intentionality in communication is indicated by persistence, whereby signallers continue to communicate by substituting original signals with new signals if the initial response to the gesture does not adhere to the goal of the signaller (Bates, Camaioni & Volterra, 1975). Communicative persistence can improve the efficiency of social bonding between two individuals because it increases the likelihood that the recipient will more accurately understand the signaller's goal and thus respond appropriately to communication, even if the initial response by the recipient does not match the signaller's goal. For instance, if the recipient is not responding in the manner matching goal of the signaller during grooming initiation, signaller can use another gesture to elicit desired response to the gesture in circumstance, when the response would be incorrect if the signaller did not produce a new gesture. Thus, in socially complex species there should be a greater need for the use of intentional communication than in socially non-complex species (Roberts & Roberts, 2018a).

(4) Referentiality

One key function of communication is to influence behaviour of the recipient by directing their movement and attention towards either the self (the reference to the signaller), other (the reference to the recipient) or the immediate environment (reference to the location in the external environment or third party). Communication is identified as referential when the referent is consistently associated with the signal form and the signal form consistently elicits a congruent response to the signal from the recipient (Seyfarth, Cheney & Marler, 1980). In instances of referential signalling, there is a coordination of attention and communication between the signaller and receiver to a referent, a goal and to one another, providing evidence that signallers act purposefully to communicate about the referent. Primate signals, such as bodily gestures and vocalisations can draw the recipient's movement and attention to the signaller (Hopkins, Taglialatela & Leavens, 2007; Leavens *et al.*, 2004; Roberts *et al.*, 2014a; Roberts *et al.*, 2012b). Furthermore, primates can draw the attention and movement of the recipient – to the recipient themselves by the use of directional manual gestures (Roberts & Roberts, 2018b). For instance, when primates are grooming, signallers sometimes indicate to recipients that they need to move a specific part of their body, in order that the signaller can groom a particular body area (e.g. for the recipient to raise their arm so the signaller can groom under their arm). Signallers can use distal, visual gestures (received through visual contact) to communicate this information and this may represent a type of referential signalling that could be viewed as having characteristics of referential pointing (e.g. 'limp extend', see video clip at www.youtube.com/watch?v=Ut3Gu9Eoqjk, Roberts *et al.*, 2014a; Roberts *et al.*, 2012b). Camaioni (1993) argued that this type of visual gesturing may have greater cognitive complexity than either tactile (received through tactile sensation) or auditory gestures (received through hearing). Visual gestures demand that the signaller sees the recipient as capable of comprehension that the interaction can be causally influenced by distal means. In contrast, tactile or auditory gestures may exercise direct causal effect on the recipient that is cognitively less complex. In this context, primates may specify information contained in distal, visual gestures by physically touching the spot to be moved by the recipient if the visual gesture was unsuccessful in conveying the goal of the signaller providing further evidence for referential nature of this type of signalling (Roberts, Vick & Buchanan-Smith, 2013). This capacity to refer to entities external to the self can increase the efficiency of social bonding by increasing the ability of the recipient to identify the goals of the signaller regarding changes in recipient's behaviour (Roberts *et al.*, 2018b). Given the greater need to coordinate social bonding activities in primates in order for the group to function as a cohesive whole (Dunbar & Shultz, 2017), we would expect to see a greater rate of referential communication in socially complex, bonded species, compared to less socially complex species.

(5) Laterality

Laterality is defined as a dominance of one side of the brain in controlling particular activities or communication (Fitch & Braccini, 2013). There is a widely documented hemispheric bias in the use of primate communication, whereby left-handed or left-sided signals are controlled through right-hemisphere and right-handed or right-sided signals are controlled through the left-hemisphere. In humans, right-hemisphere-controlled communication is more emotionally expressive than left-hemisphere controlled communication (Sackeim, Gur & Saucy, 1978). Right hemisphere-controlled communicative complexity can lead to attentional and behavioural convergence by inducing compatible affect between two interacting individuals (Owren & Rendall, 2001). In contrast, left-hemisphere-controlled communication tends to be used in evolutionarily 'urgent' contexts and can increase the communication specificity (Mutha, Sainburg & Haaland, 2010). For instance, in humans, right-handed gestures are more effective in accurately indicating the target of communication than left-handed gestures. By increasing the signaller's accuracy of movement, left-hemisphere-controlled communication can achieve the signaller's goal more effectively, improving the efficiency of social coordination. For instance, in contexts of antagonism recruitment of support from dominant individual in the group may depend on a primate ability to indicate to the dominant individual precisely that they are a target of a gesture (Video 1). Further, the signallers right-handed gestures made in the context of giving grooming can indicate more precisely to the recipient which body part they should move and this would have aided efficiency of establishment of social bonds with the recipient by reducing the risk of miscomprehension (e.g. video clip at https://www.youtube.com/watch?v=Ut3Gu9Eoqjk). Thus, the capacity to coordinate movement and attention through increased precision of indication is one characteristic of the complex cognitive skills that may lead to more complex sociality of bonded systems by improving the ability of the recipient to respond accurately to communication (Roberts, Murray & Roberts, in press). As such, we would expect that there will be a hemispheric bias in the use of communication in primate bonded systems, with different social functions controlled through right-hemisphere-controlled communication and left-hemisphere controlled communication (Sackeim *et al.*, 1978).

(6) Learning and innovation

Communication innovation (creating new signals) and communication learning (copying or modification) are two complementary processes involved in the production and usage of signals. The complexity of cognitive skills underlying these processes in primates is much debated as many different cognitive mechanisms have been proposed as being involved in innovation and learning (McGuigan, Burdett, Burgess *et al.*, 2017). However, researchers agree that these skills require a high degree of voluntary control to facilitate their operation (Ruch, Zürcher & Burkart, 2018). Learning and innovation of communicative signals give rise to the distinct patterns in the overlap of communicative repertoires, with both homogeneity (presence of the same signal in the repertoire of both signaller and the recipient) and heterogeneity (presence of the signal in the repertoire of the signaller but not in the repertoire of the recipient) occurring within and between dyads (Roberts & Roberts, 2017). For instance, signallers direct homogenous communication repertoire at the recipient who is likely to respond to communication (greater homogeneity) but differentiate from features of the communication repertoire of the recipient who is less likely to respond to communication (greater heterogeneity). This capacity to modify communication in relation to the likelihood of responsiveness of the recipient may be important for the efficiency of signalling and social bonding (Roberts *et al.*, 2017). Homogenous communication may facilitate communication comprehension by facilitating making of the perception–production link that enhances mutual understanding between interactants. Indeed, homogenous communication has been found in contexts such as mutual grooming and joint travel when social bonds have been established (Roberts *et al.*, 2017). In contrast, heterogeneous communication may contain attention-catching properties that effectively direct movement and attention of the recipient towards the signaller and these properties can in turn influence likelihood that the recipient will remember the signaller and respond to the signal (Cullen, 1966; Marler, 1961). Unidirectional grooming, for example, where capturing recipient's attention is particularly important because social bonds are weaker, is one context where heterogeneous communication has been observed (Roberts *et al.*, 2017). Since socially bonded species require a large degree of negotiation over responsiveness of the recipient, it could be predicted that this ability to innovate and learn communication would influence the ability of the signaller to maintain more complex social relationships. For instance, signallers use heterogeneous communication to build social relationships and use homogenous communication to maintain ongoing relationships. As such, we would predict greater use of differentiated homogenous and heterogeneous communication in complex, bonded species as compared with those that are less complex.

(7) Arousal control

Emotional arousal has been operationally defined as a state of physiological activation experienced as a change in heart rate (Aureli, Preston & de Waal, 1999; Boysen & Berntson, 1989), cortisol secretion (Behringer, Borchers, Deschner *et al.*, 2013; Thompson, Muller, Kahlenberg *et al.*, 2010) or nasal temperature (Kano, Hirata, Deschner *et al.*, 2016). Arousal change is associated with corresponding communication patterns, classified along the dimension of intensity or strength such as the potency of its presentation (loudness), frequency and duration (Burgoon, Kelley, Newton *et al.*, 1989). For instance, louder human voices are associated with a higher level of arousal of the signaller than quieter voices, suggesting that communication loudness can be used to indicate the intensity of arousal of the signaller (Scherer, 1982; Scherer & Oshinsky, 1977). Further, communication in itself can also alter the arousal of the recipient (Patterson, Jordan, Hogan *et al.*, 1981), in that communication associated with different levels of emotional arousal of the signaller is associated with different behavioural, physiological and fitness outcomes in the recipients (Beerda, Schilder, van Hooff *et al.*, 1998; Kano *et al.*, 2016; Wascher, Scheiber & Kotrschal, 2008). High-arousal signals trigger a range of neurological and hormonal responses associated with increased heart rate and cortisol release (Beerda *et al.*, 1998; Kano *et al.*, 2016; Wascher *et al.*, 2008), which can negatively influence the recipient's health and survival (Capitanio, Mendoza, Lerche *et al.*, 1998). In contrast low -arousal signals can have a stress buffering effect on the recipient, and therefore increase the duration of time spent in social bonding activities (Roberts *et al.*, 2016a). Flexibility in modifying arousal underpinning communication should therefore be important to regulating social relationships in bonded primate groups, but such flexibility requires greater cognitive skills than the use of a simpler communication system in an inflexible way. For instance, communication inhibition, whereby signallers suppress their pre-potent drive to express high emotional arousal through high intensity communication and instead use low intensity signals to communicate requires a high degree of voluntary control underpinning communication (Tops & Boksem, 2011). The ability to inhibit pre-potent responses correlates with neocortex volume and depends on the Brodman area 10, brain regions which underpin complex cognitive processing (Passingham & Wise, 2012). Reducing the arousal associated with communication can facilitate a greater level of responsiveness in the recipient, because it creates the perception of a positive, fitness rewarding intent of the signaller (Mendl, Burman & Paul, 2010). Thus, low intensity communication fosters trust that the relationship will not be compromised through a random act of aggression and this type of signalling may be especially important in the circumstances when the dominance relationships have been unresolved as is often the case in more egalitarian, bonded species (Maestripieri, 1999). Thus, by reducing arousal associated with communication, signallers can be more successful in eliciting a response from the signaller without resorting to higher arousal forms of communication designed to elicit a response from an unresponsive recipient (Mendl *et al.*, 2010). Whilst in many instances reducing arousal can be advantageous, increasing arousal can also demand voluntary control over communication and can be beneficial in circumstances of social bonding in complex social settings. Thus, we predict that in socially complex species there will be a greater need for arousal control underpinning communication than in socially non-complex species (Roberts *et al.*, 2016a).

(8) Rewarding communication

Primates often experience anxiety in response to uncertainty in social situations such as proximity to unpredictable social partners with whom dominance relationships have been unresolved (Aureli, 1997; Schino, Scucchi, Maestripieri *et al.*, 1988). In primates, rewarding communication may play an important role in mediating the relationships with the individuals who experience high levels of anxiety. This type of communication may create a psychopharmacological environment within which social bonds of trust develop that enhance recipient's commitment to the social interaction. For instance, a mild mechanical touch as well as more intense tactile contact (Video 2) can act as a stimulus that not only effectively influences recipient's behaviour through more intense, literal means but also has a potential to activate neural sensory afferent fibres (C fibres) involved in the release of a suite of neurohormones that act on the reward system. By the same token, high-intensity, synchronized vocalisations accompanied by loud, rhythmic, auditory gestures such as drumming (Video 3) or clapping (https://www.youtube.com/watch?v=-T8qJ9D1-g8) can trigger the release of social neurohormones on a larger scale similar to those released by tactile gestures (Chanda & Levitin, 2013). By relieving recipient's anxiety through increasing pleasure from the interaction, rewarding communication is hypothesized to draw recipient's attention onto the signaller and elicit their commitment to the ongoing social behaviour (e.g. grooming or travel) by increasing their responsiveness. We predict that in socially complex species there will be a need for primates to engage in rewarding, dyadic one on one communication and also synchronized communication (Roberts *et al.*, 2016b).

b**) How increases in complexity of cognitive skills underpinning primate communication would have facilitated complex sociality?**

Social characteristics of primate groups differ across number of dimensions but perhaps the most important dimension is the degree of influence of kinship on intraspeciic social dynamics. In many primate species, distribution of affiliative behaviour and agonism (aggression and alliances) is strongly influenced by kinship, in that affiliation occurs mainly within clusters of kin, whereas agonism is more common between unrelated conspecifics (Maestripieri, 1999). In these species, there may be less pressure to develop complex communication because there is a greater degree of influence of olfaction and hormonal priming on intraspecific affiliation. In contrast, in primate species where the influence of kinship on intraspecific social dynamics is reduced, affiliation is not limited to clusters of kin and can occur between any unrelated dyads. This means that a redundancy in hormonal priming for affiliative behaviour demands more complex communication skills. In these societies, complex communication facilitates formation of social bonds with unrelated and less familiar conspecifics and this has a profound influence on individual success in the group and fitness (Maestripieri, 1999). Hence the cognitive skills underpinning communication will not be uniform across all primates, but will vary according to the extent to which different primate species are less reliant on kinship and therefore require more complex communication for the maintenance of the social system. In this section we outline different ways in which more complex cognitive skills underpinning primate communication may have facilitated increases in complexity of social relationships (Table 1).

(1) Group size

Within primates, large groups are assumed to be more socially complex than small groups, as there are more relationships to track, and individuals must spend an increasing amount of their time servicing their social relationships, in order to enable large groups to function as stable, functional cohesive units (Dunbar *et al.*, 2007). However, there is currently no standard way to compare social complexity across groups of different sizes, and we have little understanding of how the patterning of social relationships changes with increasing group size. In smaller groups, primates may be able to form relatively strong ties with all group members, with frequent interactions based on multiple different behaviours such as grooming, facial expression, gestures, vocalisations and proximity. However, as group size increases, the ties primates have with other individuals will become increasingly weak. These weaker, indirect ties are cognitively complex to manage, and this is especially true in fission-fusion social systems, where the frequency of interaction between two individuals will be much lower than in stable groups (Barrett, Henzi, & Dunbar, 2003). Thus, in larger groups one may predict that there will be an increasing need for flexibility in communication. Namely, primates must be able to flexibly use different communication strategies and behaviours to maintain ties of weaker strength. Thus, if cognitively complex communication is more effective at managing bonded social relationships than cognitively less complex communication, then in large social groups it could be predicted that there would be increased communicative complexity (e.g. intentionality, rewarding property), because of the need to use increasingly sophisticated strategies to maintain an increasing number of weaker ties. Finally, it could be predicted that the structuring of the group may change, with an increasing number of sub-groups forming in larger groups.

(2) Temporal and spatial stability of social system

One of the main variations in different social systems is in the degree of temporal and spatial stability shown in group size and composition. In fission-fusion social systems the broader group or community changes its size by means of the fission and fusion of subunits (known as parties or sub-groups) according to both the activity (e.g. resting, feeding) and distribution of resources (Aureli, Schaffner, Boesch *et al.*, 2008). The term fission-fusion dynamics refers to the extent of variation in spatial cohesion and individual membership in a group over time (Amici, Aureli & Call, 2008). Some animal groups have a low degree of fission-fusion dynamics in that the membership of the group is temporally and spatially stable, and thus all individuals will typically encounter every member of the group every day (Aureli *et al.*, 2008). In contrast other animal groups have a high degree of fission-fusion dynamics (Aureli *et al.*, 2008). In these groups, individuals form socially and geographically circumscribed communities, within which they associate in temporary subgroups ('parties') that vary in size, composition and duration (Amici *et al.*, 2008). Individuals in the wider community may thus only see each other at infrequent intervals, often weeks apart, but each individual can recognise members of their own community and is capable of maintaining long-term relationships with these individuals (Barrett *et al.*, 2003). Tracking these indirect relationships is hypothesised to be cognitively demanding, as in fission-fusion systems individuals must be able to retain and manipulate information about others whom they see only infrequently, as compared to systems with groups that are stable spatially and temporally where members see each other every day (Barrett *et al.*, 2003). Thus fluid fission-fusion system and stable, cohesive groups are at opposite ends of a continuum of social organisation.

In both fission-fusion and stable social systems, primates maintain stable, long lasting social relationships. Thus, in both fission-fusion and stable social systems, individuals use multiple different behaviours such as grooming, facial expression, gestures, vocalisations and proximity to maintain their social relationships. However, in a fission-fusion social system, the time and cognitive demands behind managing multiple social relationships based on irregular interaction implies that the social bonds are weaker, as individuals encounter each other less often (Barrett *et al.*, 2003). Thus in a fission-fusion social system there may be a greater need for flexibility in communication, relative to a stable social system. Specifically, in fission-fussion social systems, there should be a greater ability to maintain bonded relationships flexibly through cognitively complex communication, as seen in a greater dissociation between networks based on different measures of behaviour (e.g. grooming, vocalisations, gestures, intentional communication, rewarding communication).

In addition, group size influences the underlying social structure and changes patterns of communication, so understanding the influence of group size is important in examining the influence of social organisation on the level of social complexity individual animals have to deal with. Increasing group size in a stable species will result in individuals simply encountering more individuals each day, whereas increasing community size in the fission-fussion species will result in the animals having to keep track of more indirect relationships with whom interaction may be infrequent (Barrett *et al.*, 2003). Thus, the influence of group size on the patterning of social relationships should be greater in fission-fusion than stable groups, as there is a greater need for differentiated communication in fission-fusion compared to stable social systems.

(3) Group density

In denser groups, where the number of individuals who are in direct close proximity is greater than in less dense groups, the number of third party social relationships that individuals must track increases (Dunbar *et al.*, 2007). Thus we can predict that it will become increasingly difficult for an individual to adjust their behaviour in denser groups, and that primates in denser groups will therefore demonstrate an asymptotic limit on how many social relationships they can track. For instance, in denser social groups, the difficulty of adjusting behaviour to a large number of third party relationships may precipitate the evolution of broadcast communication that can bond interactants on a larger scale, without the need for dyadic one on one social bonding (Roberts *et al.*, 2016b). In particular, gestural communication in primates exhibits greater flexibility than vocal communication, and this may be shown in the extent to which primates are capable of using gestures and vocalisations flexibly according to the social situation (Corballis, 2003; Fitch, 2010;

Killin, 2017; Sterelny, 2012). Examining how the density of social groups is associated with communicative complexity can thus provide insight into the cognitive complexity involved at the micro-level of managing social relationships.

(4) Member roles

The position and network characteristics of individuals vary by age, sex and dominance rank, meaning that these characteristics affect the patterning of social relationships, and the roles that different individuals play in the group as a whole. However, there is considerable variation in the extent of the sex, age and rank differences in sociality in different populations of primates (Lehmann & Boesch, 2008). For instance, in large groups which form because the risk of mortality or injury is high, vulnerable individuals may stay in closer proximity to dominant 'protector' males, party spread may be reduced and proximity between individuals increased (Altmann, 1979; DeVore & Washburn, 1963; Hockings, Anderson & Matsuzawa, 2006; Otali & Gilchrist, 2006; Reynolds, 1963). However, with increasing group size there is a tendency to reduce proximity and mutual visual contact, as the social bonds are weaker. Thus, the need to strengthen social bonds with 'protector individuals' in order to reduce mortality may drive the need to develop differentiated communication strategies by vulnerable group members that increase social cohesion in these contexts. The role individuals play in the network will influence the number and type of signal recipients and hence the demands of tracking differentiated social relationships, which may be reflected in the type and complexity of communication used by a signaller. For instance, protector individuals track many social relationships of group members and to reduce these demands, vulnerable individuals may use strategies that reduce the cognitive load of protector individuals by using communicative strategies that facilitate involuntary recall of information about their individual identity (e.g. use of mutual visual contact) (Conty & Grèzes, 2012; Roberts *et al.*, 2017; Roberts *et al.*, 2018b). When individuals play many different roles in the network, there may be a greater need for more complex communication to differentiate between different types of social relationships and this will be particularly important with increasing group size.

(5) Egalitarian structure

In primate societies, a distinction can be made between 1) despotic social relationships based on a strong influence of the dominance hierarchy, where the dominant individual always supplants or antagonizes the subordinate individual over access to resources, but is never supplanted or antagonized by the subordinate and; 2) egalitarian social relationships where the influence of social hierarchy on social relationships is weaker and thus social partners are equally likely to supplant, antagonize and win if engaged in a fight over access to resources (Goodall, 1986). In despotic species, signallers know the likelihood other conspecifics will win in contests over access to resources and therefore despotic relationships increase certainty by having predictable outcomes (Ay, Flack & Krakauer, 2007; Flack, Girvan, De Waal *et al.*, 2006). Maintenance of social structure can be achieved by special signals which show the signaller's consensus for the dominance status of the recipient (Ay *et al.*, 2007; Flack *et al.*, 2006). In contrast, in egalitarian species, the likelihood of winning is not known in advance, resulting in high levels of uncertainty. Social coordination is driven by communication that demands high levels of flexibility to resolve ambiguity over one's access to resources. The presence of third party audience may add another challenge to these interactions, in terms of inferring the potential of a partner to recruit support from the audience when competing for access to resources. Thus despotic and egalitarian social relationships will differ in the complexity of cognitive skills underpinning communication, in terms the need to incorporate knowledge of past relationships and the behavioural context when deciding how to communicate.

(6) Dispersal

Social groups of primates are different to those of other mammals by having distinct layers of social structure (Hill, Bentley & Dunbar, 2008; Kudo & Dunbar, 2001; Roberts *et al.*, 2016a;

Roberts *et al.*, 2016b). One important factor that influences the partner preferences that create these layers of social structure, is whether individuals remain faithful to their natal breeding site or group. In mammals it is usually males who disperse rather than females (Greenwood, 1980). Male dispersal leads to enhanced opportunities for female social bonding, meaning that among mammals, male-bonded social systems are rare. Hence, it has long been acknowledged that the defining feature of mammal sociality is female-bondedness (Lehmann & Dunbar, 2009). In particular, related females form stable social groups in almost all of the Old World and New World monkey species. However, most socially and cognitively complex primates (i.e. great apes such as chimpanzees, bonobos, gorillas and humans) are based on male-bondedness, as females disperse (Greenwood, 1980). Unlike in female bonded groups, primates in male bonded groups form equitable social bonds that are cognitively demanding in terms of remembering previous experiences with the partner, making decisions about how to compete based on small differences in resource holding potential, and in recognizing relatedness in the absence of shared history of association with the mother (as the majority of the males are paternally related). Managing these social relationships ineffectively may have severe consequences, in terms of a high risk of injury or death as result of physical conflict. These social relationships may demand a subtle appreciation of others intentions and greater communicative complexity. Thus, primates who evolve skills of complex cognition underpinning communication can evolve a more complex bonded system than other mammal species.

(7) Mating system

In some mammals, females form an enduring, life-long ‘pair bond’ with the mating partner. In some taxa, these types of relationships have been seen as a baseline of social complexity (primates: Dröscher & Kappeler, 2013), whereas in others, they have been considered as a very complex form of sociality (bats: Pitnick, Jones & Wilkinson, 2005; ungulates: Shultz & Dunbar, 2005). Whereas pair-living may be viewed as simple form of sociality due to the small number of social relationships that have to be maintained, the bonded type of social relationship requires a number of communication skills that are cognitively demanding. These include for example, subtle coordination through low intensity signals that requires a greater ability to voluntarily modify the arousal underpinning communication, in order to successfully manage relationships in repeated social interactions. Furthermore, due to the memory of the past interactions and familiarity, pair-bonded partners have a much more subtle appreciation of each other's needs and intentions, and ability to respond to low intensity signals. The cognitive complexity of communication that is needed to maintain bonded relationships should therefore be reflected in larger brains of pair-bonded species, relative to other species in the same order. For instance, when group size is partialled out, pair-bonded species have larger brains and especially neocortex, than species living in very much larger social groups where relationships are less intense, less structured and more casual, suggesting that cognitive demands behind complex communication may drive the link between pair bonding and cognitive skills (Shultz & Dunbar, 2010; Shultz & Dunbar, 2007).

IV. A BRIEF REVIEW OF EVIDENCE FOR COMMUNICATIVE ROOTS OF COMPLEX SOCIALITY AND COGNITION

To date, partly because the primary medium of human language is vocal, research in animal communication has mainly examined important aspects of primate cognitive abilities in relation to the vocal communication systems (Tomasello & Zuberbühler, 2002). The evidence suggests that primates may have complex cognitive abilities indicated by functionally referential calls in many primate species that can reliably provide recipients with information about the presence of predators or food in the environment (Zuberbuhler, 2009). For instance, vervet monkeys use different alarm calls in association with different predators leading to different escape responses in recipients; perceiving the call or the predator itself elicits the same specific response (Seyfarth *et al.*, 1980). Chimpanzees in captivity produce acoustically different food grunts in response to quality of the food eaten (Slocombe & Zuberbuhler, 2005; Slocombe & Zuberbuhler, 2006).

Additionally, there is evidence in vocal communication for audience effects, where the signaller's vocal behaviour is affected by social characteristics (such as relative dominance or familiarity) or the presence or absence of conspecifics. For instance, Gouzoules and colleagues (1984) have shown that rhesus macaques produce acoustically different scream variants as a function of aggression severity, relatedness and the relative rank of the opponent.

However, whilst receivers can infer referents from signaller's calls, there is less strong evidence that vocalisations are intentional from the signaller's perspective. Thus, whether signallers attempt to inform others about the presence of external referents, or whether vocalisations express the emotional state of the signaller, is still a topic of intense debate (Crockford, Wittig, Mundry *et al.*, 2012; Fischer, 2017). For instance, vervet monkeys continue producing alarm calls even after the recipients have responded to the signal (i.e. the monkeys have already escaped to safety) (Seyfarth *et al.*, 1980). Chimpanzees continue producing loud pant-hoot calls upon finding patches of food even if the whole community is already feeding on the food tree (Clark & Wrangham, 1994). The findings from vocal development in primates also indicate that certain cognitive skills in vocal domain may be more constrained. Although primates can modify existing call types to match those of the partner (Watson, Townsend, Schel *et al.*, 2015), there is ample evidence for the inability of primates to invent and acquire new sounds from other individuals. For instance, cross-fostering of Rhesus monkeys and Japanese monkeys produces no significant changes in the repertoire or structure of their species-typical vocalisations (Owren, Dieter, Seyfarth *et al.*, 1992). Additionally, language-trained apes subjected to years of language instruction are unable to acquire any substantial vocabulary of words (Hayes & Hayes, 1951). This reduced breadth of cognitive skills in the vocal domain of communication does not reflect overall limitations of primate cognition, but rather the difficulty of the communicative mechanism to control vocal output (Lieberman, 1968). Whilst the basic vocal tract anatomy of primates would support production of complex sounds, and is likely to do so in low intensity calls, the neural abilities responsible for detailed voluntary control of the vocalisations and the capacity to link auditory input to corresponding motor outputs are less robust in our primate relatives (Jurgens, 1998). Given the limitations of the previous findings on cognitive skills underlying vocal behaviour (Fischer, 2017), it is perhaps unsurprising that the cognitive skills underpinning vocalisations have not yet been related to sociality. One notable exception to this general pattern is the demonstration of the link between vocal repertoire size, group size and brain size across primates (McComb & Semple, 2005). The research showed that the size of the vocal repertoire in primates is associated with brain size suggesting that the cognitive demands behind managing more complex relationships in large social groups precipitated evolution of large vocal repertoire and brain size.

Whilst features of cognition make primate vocalisations an unlikely sole candidate for an evolutionary driver of primate bonded social system, it is possible that the cognitive skills underlying social evolution are also present in the gestural modality of communication (Burling, 1993; Corballis, 2003; Hewes, 1992). This is because primates have a greater voluntary control over their limbs than their vocal output and more important similarities with human communication can be observed in the gestural modality in many areas of cognition such as learning, symbolic communication and intentionality (Tomasello & Zuberbühler, 2002). For instance, whilst vocal culture has not yet been shown among any of the primate species (Pollick & de Waal, 2007), gestural cultures have been reported both in the wild (see e.g. hand clasp, leaf clipping) (McGrew & Tutin, 1978; Whiten, Goodall, McGrew *et al.*, 1999) and in captivity (Tomasello *et al.*, 1985). Additionally, whilst primates display an inability to learn vocal modifications, they have ability to acquire and use symbolically many gestures of American Sign Language, which they are then able to transmit culturally to their offspring (Gardner, Gardner & Van Cantfort, 1989; Menzel, 1999). Moreover, primates do not appear to use their calls intentionally (but see Crockford *et al.*, 2012 for possible evidence of this) whereas they have an ability to interact intentionally in their interactions with humans (Cartmill & Byrne, 2007; Leavens, Russell & Hopkins, 2005; Roberts *et al.*, 2014b) and with conspecifics (Roberts *et al.*, 2018a; Roberts, Vick & Buchanan-Smith, 2012a; Roberts *et al.*, 2013).

When exploring the link between cognitive skills underlying gestural communication and sociality, manual gestures, defined as communicative movements of hands without using or touching objects, are particularly important. This is because manual gestures are neurologically distinct from other types of gestural communication, such as bodily movements and locomotory gaits. Broca's area is a region of the hominid brain with functions linked to human communication (Broca, 1861). The ape Brodmann's area 44, which is homologous with humans Broca's area, is enlarged in the left hemisphere (Cantalupo & Hopkins, 2001). In contrast to vocalisations, the monkey's Brodmann's area is activated during both the production and perception of manual movements (Rizzolatti, Fadiga, Gallese *et al.*, 1996). These neural structures underlying manual gestures in the great apes are homologous with the communication areas in the human brain, suggesting an important link between human communication and primate manual gestures, but not primate calls or other primate bodily movements (Corballis, 2003). Additionally, while many primate species commonly communicate with calls, facial expressions or bodily movements, manual gestures are typically widely used only in humans and other great apes (Byrne, Cartmill, Genty *et al.*, 2017; Pollick & de Waal, 2007). This lack of homology between Hominoidea and all other primate species regarding manual gestures, indicates a shift towards a more flexible and intentional production of manual gestures in our pre-hominid ancestors (Corballis, 2003) which may have facilitated the emergence of complex social system.

Most of our knowledge about the link between sociality and gestural communication comes from studies of gestural behaviour in chimpanzees, as this is the great ape species whose gestural communication has been most intensively studied (Byrne *et al.*, 2017; Hobaiter & Byrne, 2014; Pika & Mitani, 2006; Roberts *et al.*, 2014a; Tomasello & Frost, 1989). For instance, the gestural communication of the Sonso group of Budongo (Uganda) in East Africa, with a special focus on adults, was described by Roberts and Roberts (2016b). They found that gestural communication is associated with the duration of time spent in proximity. Use of visual gestures combined with hand extensions and low intensity calls (Video 4) occur at a higher rate between individuals who spend longer periods of time in proximity. In contrast, tactile and auditory gestures unaccompanied by these behaviours occur between individuals who spend shorter periods of time in proximity (Roberts *et al.*, 2018b). These observations were later supplemented by observations of intentional use of gestures in relation to proximity (Roberts *et al.*, 2018a). Chimpanzees that spent longer periods of time in proximity used persistence sequences at a higher rate, as compared to chimpanzees that spent shorter periods of time in proximity. Moreover, recent studies showed that a larger repertoire of gestural communication occurs between dyad partners who spent a longer duration of time in proximity, as compared to dyad partners who spent a shorter duration of time in proximity (Roberts, Chakrabarti & Roberts, 2019). Further, chimpanzees who spent shorter periods of time in proximity appear to engage in rewarding communication more often than the chimpanzees who spent longer periods of time in proximity (Roberts *et al.*, 2018a). Chimpanzees produce 'synchronized high intensity panthoots' (Video 3) – a form of communication where loud auditory gestures (e.g. drumming made by hitting tree trunk with the feet) are responded to by the joint vocal reaction of a wider audience (Roberts *et al.*, 2016b). Chimpanzees also produce tactile gestures that can be responded to by turn-taking episode of visual or tactile gesture (Video 2) (Roberts *et al.*, 2018a). Both of these communication types appear to occur between pairs of individuals that spent a short time duration in close proximity (Roberts *et al.*, 2018a; Roberts *et al.*, 2016b). These behaviours are shown to reduce anxiety in recipient, thus influencing social bonding.

From this, it follows that chimpanzees can flexibly modify their communication in relation to the duration of time they spend in proximity to others. Differentiation in communicative strategies in relation to proximity shows that chimpanzees have social awareness, and can gesture flexibly in relation to the strength of the social bond with the partner (Schneider, Liebal & Call, 2017). However, the more informative source of data in regards to the link between social and communication complexity comes from examining the communicative underpinnings of bondedeness, or degree to which chimpanzees engage in social interactions directly. These data demonstrate that bonded relationships based on reciprocated grooming in larger parties are maintained through cognitively complex communication more effectively than through less cognitively complex signalling. Right handed gestures are believed to be more cognitively complex than left handed gestures because they are linked to greater cortical control over motor actions in terms of ability to learn and flexibly adjust manual movement, enabling more effective comprehension and learning of communication by the recipient (Mutha, Haaland & Sainburg, 2012). When social bonds are weaker, meaning dyad partners are not engaged in mutual grooming, right handed gestures are more likely to elicit a response and reciprocity to grooming, relative to left handed gestures (Roberts *et al.*, in press).

Right handed gestures are particularly important in maintaining bonded relationships in complex social settings. The bonded social relationships in average parties that have a size of five individuals for East African chimpanzees appear to be maintained through left handed visual gestures. Since the interests of the signaller and the recipient in social bonding in these parties coincide, chimpanzees use low intensity, visual left-handed gestures to manage social relationships (Dawkins and Guilford 1997). However, when the complexity of the social setting increases, monitoring of third party audience can cause distractions in the joint attention between the signaller and recipient. In turn, this leads to a decrease in social bonding, as measured by mutual visual attention, mutual grooming and proximity between the signaller and the recipient (Roberts, 2018). When the size of the party increases from approximately five individuals to eight individuals, visual right-handed gestures can enable social bonding in this more complex social setting. As the size of the party reaches thirteen chimpanzees, signallers adapt to the increasing social complexity by increasing their reliance on more intense left-handed gestures (tactile, auditory) that incorporate a rewarding property in signalling and exploit similar mechanisms to grooming. This also suggests that as the number of social bonds based on reciprocated grooming increases, it eventually reaches an asymptotic limit where no more of these types of relationships can be maintained in larger social parties, due to time and cognitive demands of maintaining them (Dunbar, 2018). In order to overcome this limit, chimpanzees may use rewarding gestures to facilitate social interactions in the absence of reciprocated grooming. By having rewarding properties, these gestures facilitate greater social complexity by redirecting the recipient's attention away from the wider audience and back onto the signaller. This means that signallers can coordinate social interactions such as travel more effectively, as compared to other types of signalling. Another piece of evidence in support of the notion that bondedness in complex social settings is facilitated by cognitively complex signalling comes from examining the link between communicative persistence and sociality. Recent data shows that in larger parties where the social bonds are weaker and the chimpanzees engage in mutual grooming for shorter periods, communicative persistence facilitates bonded relationships based on grooming (Roberts, 2018). This research clearly shows how cognitively complex behavioural strategies can shape social bonding in response to increases in social complexity.

Whilst we have increasingly good insight into various aspects of cognitively complex communication in relation to complexity of sociality, the lack of ability to infer causality in observational studies may make it difficult to draw inferences about the presence and form of communication that facilitated life in complex social groups in our hominin ancestors (Fitch, 2005). Some of the most compelling evidence of the influence of cognitively complex communication on social coordination comes from the experimental studies of language-trained apes. In a task that required use of communication to obtain hidden food that could not be obtained individually, language trained chimpanzees using communicative persistence to correct experimenters understanding about location of hidden food were able to obtain the food much faster, as compared to chimpanzees who did not use such complex communication (Roberts *et al.*, 2014b). Since social coordination of dyadic one-on-one interactions gives rise to social groups, these results suggest that more complex social structure can emerge through cognitively complex behaviour. These findings are consistent with the hypothesis for communicative roots of complex sociality and cognition: as the complexity of cognitive skills underpinning communication increased, we would predict primate species living in more complex, structured social systems.

Whilst there is clear evidence of flexibility in primate gestural communication (Byrne *et al.*, 2017; Schneider *et al.*, 2017), there is still a debate as to the cognitive underpinnings of this flexibility in communication, and the cognitive abilities of non-human primates in general. Some researchers claim non-human primates, and particularly some great ape species have the ability to understand mental states in others (Krupenye, Kano, Hirata *et al.*, 2016), but others are more sceptical of such claims, arguing that behaviour that appears complex can have relatively simple cognition underpinning it (Barrett, 2016; Fischer & Price, 2017; Heyes, 2017; Leavens, Bard & Hopkins, 2017). For example, Fisher and Price (2017) argue that whilst primate vocalisations and gestures do appear to be goal-directed, there is a lack of evidence of communicative intent and propose that this is in line with the lack of solid evidence of mental state understanding. In turn receiver's use signals to predict the signaller's behaviour, leading to a flexible communication system that is not underpinned by higher-level mental state understanding from either the signaller or the receiver. This view is consistent with the studies that showed relative difficulty of identifying theory of mind in primates such as evidence for false belief (e.g. chimpanzees, Call & Tomasello, 1999; Hare, Call & Tomasello, 2001; Kaminski, Call & Tomasello, 2008; chimpanzees, bonobos, human children, Krachun, Carpenter, Call *et al.*, 2009) and deception (capuchin monkeys, Wheeler & Hammerschmidt, 2013). More broadly, Barrett and colleagues (2007) suggest that much of primate behaviour is based not on long-term durable social bonds between pairs of individuals underpinned by conceptual knowledge of these relationships that persists through time. Instead, Barrett et al. (2007) argue that primates make moment-by-moment adjustments to the current social situation, using social contact and proximity to achieve their immediate goals. For example, coalition formation among free-ranging male vervet monkeys appears to be opportunistic, allowing pairs of monkeys to target a conspecific with a reduced risk of injury, and there was little evidence of long-term strategic advantage to the coalition partners in terms of fitness benefits or an increase in rank (Freeman, Young, Barrett *et al.*, 2016). Finally Leavens and others (2017) notes the inherent difficulty in formulating hypotheses and interpreting behaviour based on unobservable mental states, and argue that future studies should define mental states purely in terms of behaviour and context, as this is all that can be measured objectively and scientifically. Overall, therefore there is still ongoing debate both with regard to primate communication and primate cognition more generally as to the evidence for higher-level cognitive process in primates (intentionality in communication, mental state understanding) and the utility of these concepts in studying primate behaviour and communication.

V. USING SOCIAL NETWORK ANALYSIS TO EXAMINE THE LINK BETWEEN COMMUNICATION, COGNITION AND SOCIALITY

To assess how communicative and cognitive complexity varies across different levels of social complexity such as groups of differing sizes and with different levels of fission-fusion dynamics requires a systematic way of defining and measuring and comparing social complexity across groups and species. Currently, there is a lack of such a standardized measure of social complexity and developing such a measure that can be applied across different species has been described as the 'grail of social analysis' (p. 20, Whitehead, 2008). Social network analysis can be used to develop such a quantitative measure that can be applied across a wide number of primate and non-primate species. A network models a system composed of individual components ('nodes') and their connections ('ties'). Recent advances in computing power, in mathematics and statistical physics and in the availability of large-scale electronic databases have resulted in new paradigms for the characterisation of the structure of complex networks in a range of fields, including electrical power grids, transport systems, the world wide web and metabolic reaction networks (Watts, 2004). There is also an increasing realisation that network analysis - by providing common techniques and modes of analysis - can lead to a greater synthesis across the many disciplines in the mathematical, biological and social sciences in which network-related problems arise.

In social networks analysis, each node usually represents an individual, and each edge (or, as used in this proposal 'tie') represents some measured social interaction or association (e.g. time spent grooming). The social network approach is grounded in the notion that the patterning of ties in which individuals are embedded has important consequences for these individuals. Network analysis provides a way of exploring how individual social relationships build up to produce the social structure observed at the group or population level. Understanding this link between individual behaviour and population-level phenomena is a long standing challenge in ecology and evolutionary biology (Croft, James & Krause, 2007). Network theory provides novel insights into the properties of social structure in groups that are not possible either by considering the interactions between pairs of individuals in isolation, or by studying the average properties of the group as a whole (Croft *et al.*, 2007; Wey, Blumstein, Shen *et al.*, 2008a).

Further, recently developed methods for identifying natural subgroups in networks provide a way to assess intermediate-level groupings, defined as groups of individuals that associate with each other more than with other individuals in the network. These structures may be especially difficult to detect in fission-fusion systems where group membership is unstable over time and space. Thus, using network analysis, subgroups of individuals that preferentially associate with each other could be identified within the larger social group, thus revealing the internal structure of the group in a way that would not be possible purely based on individual relationships or association indices.

Network analysis therefore provides a well-developed and established set definitions and quantitative measures (based on explicit mathematical formulae) for objectively characterising both individual relationships and social groups. As many of the measures can be standardized by dividing by group size, systematic comparisons between different groups and species can be made (Sundaresan, Fischhoff, Dushoff *et al.*, 2007). Using these quantitative measures of relationships, statistical models about social relationships and social structure can be tested (Wey *et al.*, 2008a). By comparing networks both within and between species, network methods help to determine the extent to which social structure is driven by ecology or phylogeny (Sundaresan *et al.*, 2007).

VI. THE NOVELTY OF APPLYING SOCIAL NETWORK ANALYSIS TO THE STUDY OF COMMUNICATIVE ROOTS OF COGNITIVE AND SOCIAL COMPLEXITY

The novelty of applying social network analysis to the study of communicative and cognitive complexity in relation to social factors lies in three areas. First, until recently social network analysis has not been applied to the study of animal societies, although recent review papers have noted the vast potential of network analysis to enhance our understanding of social systems and the evolution of sociality in animals (Krause, Croft & James, 2007; Wey, Blumstein, Shen *et al.*, 2008b). Thus there is a need to apply the recent advances in network analysis to the study of primates in the wild. A particularly novel aspect of this line of research may lie in the use of weighted and directed ties in the network analyses. In weighted, directed networks a numerical value reflects the strength of the tie, and there is the possibility of asymmetry in the ties. In contrast, the great majority of network analysis in social sciences, biological sciences and mathematics use binary networks, where the tie between two nodes is classified as present (1) or absent (0). The use of weighted ties is challenging, as the techniques of analysing - and in particular comparing - weighted networks are less well established than those using binary networks, and work on weighted social networks in animals is in its infancy. However, the use of weighted networks, and the comparison between weighted networks of different sizes and in different species, has the potential to open up a major new field of research in network analysis that would be applicable in many different disciplines across the biological and social sciences. This would represent a major advance on the current reliance on binary network analysis.

Second, most studies of primate relationships, in the wild or in captivity, focus on one aspect of behaviour, such as grooming or vocalizations. However, to develop a real understanding of social bonds in primates, several measures of the relationship are needed. As well as grooming, primates use visual attention to monitor conspecifics, communicate with conspecifics through both vocalisations and gestures and also preferentially associate with others through proximity. All these modes of interaction go into forming social relationships (Hinde, 1976). Thus studies which only focus on one aspect may miss important features of social relationships. Thus there is an urgent need to use data on all these types of interactions, and analyze them using network analysis. The extent to which these measures produce similar or different social networks may then be used as an indicator of social complexity. In a complex social system, individuals may need to use a variety of different behavioural interactions (grooming, vocalisations, gestures, proximity and visual attention) to manage social relationships, whereas in less complex social systems individuals would use fewer types of behavioural interactions to manage their relationships.

Third, by comparing primates with different social systems, comparisons will be possible both within species (small, medium and large groups) and between species with very different social systems (fission-fusion vs. stable cohesive groups). Network analysis provides a rigorous and systematic way of describing the networks and carrying out the comparisons at the level of individual relationships, community structures that form the building blocks of the network and global descriptors of the entire network (Croft *et al.*, 2007; Krause *et al.*, 2007).

This line of research would open up new opportunities for research in several areas. Developing models of social networks in primates offer the possibility of developing species-neutral measures of social complexity, something that is sorely lacking in current comparative studies of social structure (Wey *et al.*, 2008b; Whitehead, 2008). This measure - or more likely series of measures - can then be used to assess social complexity in a wide variety of species, both human and non-human. The cognitive complexity involved in living in different size groups and in different types of social systems can thus be determined.

Further, whilst much progress has been made assessing the archaeological record, the study of hominin social life is in its infancy (Dunbar, Gamble & Gowlett, 2014). As hominins are likely to have been characterised by a fission-fusion social system, and one of the trends in human evolution is of increasing group size over time, understanding how social network structure changes with increasing group size, and how this is affected by the social system, provides valuable insights into the evolution of human sociality. Network analysis provides new methods and a new approach with which to examine the archaeological record, with the focus on nodes (individuals or groups) and the ties (e.g. exchange of material culture, ideas, mates) between them. The network approach is just starting to be applied to human evolution, and this project will provide both the methods, and the comparative framework of how social networks operate in primates, to allow the potential of this network approach in the study of human evolution to be realised.

Finally, a detailed understanding of the social structure of primates will aid in conservation management, and an assessment of how they are likely to react to changes in habitat through deforestation or climate change. Many primate species are classified as endangered, meaning that they are considered to be facing a very high risk of extinction in the wild. For instance, there are only around 700 mountain gorillas surviving today, all in the wild and a recent survey has demonstrated an alarming fall in the population of wild chimpanzees. An urgent priority is thus to assess how future changes in habitat are likely to affect the social structure and long-term viability of primate species, to allow for effective planning of management and conservation strategies. How the social structure will change is dependent on the nature of the social network, the role of key individuals within the network and the flexibility inherent in terms of both group size and social system (e.g. level of fission-fusion dynamics). A detailed understanding of the social networks of primates will provide an invaluable tool in ensuring a long-term future for our closest living relatives.

VII. CONCLUSIONS

(1) Although much progress has been made in assessing the archaeological record, our understanding of hominin social life is in its infancy. Primates are our closest living ancestors, and

as such an improved understanding of the forces governing their sociality is important for providing valuable insights into human social evolution (Aureli *et al.*, 2008; Byrne *et al.*, 2017).

(2) Fission-fusion dynamics characterise chimpanzee and bonobos, and also are typical of modern-day hunter-gatherer (Aureli *et al.*, 2008). This suggests that fission-fusion dynamics were characteristic of the social system of the last common ancestor of chimpanzees, bonobos and modern humans (Aureli *et al.*, 2008). Further, a general trend in the course of human evolution is an increase in brain size, and this is likely to have been accompanied by a corresponding increase in social group size (Aiello & Dunbar, 1993). However, the information processing demands that drive the corresponding increase in brain size and group size are currently unclear.

(3) We propose that cognitive demands behind the communication needed to maintain bonded social groups, is a key factor in explaining the link between social complexity and cognition. In particular, we emphasize that manual gesture was a key innovation that led to more complex social systems of primates. We provide first comprehensive review that explains why complexity of cognitive skills underpinning communication is important for maintaining social bonds relative to cognitively less complex communication. We provide information about set of recent advances that suggests that communication increasing bondedness (e.g. intentionality, referentiality, rewarding communication) when the social bonds weaken (e.g. mutual grooming, close proximity, grooming reciprocity decline) enables primates to maintain social relationships in complex social settings (e.g. larger groups).

(4) To date there is no evidence how complexity of cognitive skills underlying communication varies as a function of social complexity at level of group of social system. A comparison of social complexity (e.g. stable and fission-fusion societies) offers the opportunity to explore the challenges involved in regulating social relationships in more complex, as compared to less complex social groups, and how this complexity changes in groups of different sizes. This will help us understand how the social structure is likely to have changed with increasing group size in the fission-fusion

system of early hominins, and the cognitive complexity involved in managing groups of increasing size. Further, it will help to elucidate origins of language.

(5) To carry out both the within and between species comparisons, we propose use of social network analysis, which provides a novel way to describe and compare social structure. By applying social network analysis a new, systematic way of comparing social complexity across species can be achieved, something that is lacking in current comparative studies of social structure. Given a fission-fusion system is likely to have characterised hominins, a comparison of the social and communicative complexity involved in fission-fusion and more stable social systems is likely to provide important new insights into human brain size evolution.

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Supplementary Information

Video 1 – Stretched extend gesture made with right-hand towards the dominant individual during aggressive event

Video 2 –Chimpanzee is responding with tactile communication to the gesture

Video 3 – Synchronized high intensity panthoot with drumming

Video 4 – Arm extension combined with visual gesture ('lower back')

Fig. 1 The link between complexity of cognitive skills underpinning communication and social complexity

Table 1. Link between cognitive complexity underpinning communication and social complexity