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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 was 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 forming and maintaining social relationships 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 cognitive demands behind the communication needed to form and maintain bonded social relationships in complex social settings drives the link between brain size and sociality. We review the evidence in support of this hypothesis and why key features of cognitively complex communication such as intentionality and referentiality should be more effective in forming and maintaining bonded relationships as compared with less cognitively complex

communication. Exploring the link between cognition, communication and sociality provides insights into how increasing flexibility in communication can facilitate the emergence of social systems characterised by bonded social relationships, such as those found in non-human primates and humans. To move the field forward and carry out both within- and among-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.

Key words: complex sociality, cognition, social bonding, social evolution, communicative complexity, primates, brain size, social network analysis.

CONTENTS

I. Introduction

II. Historical approach

III. Communicative roots of complex sociality and cognition

(1) Prediction 1: primates will have more cognitively complex communication underpinning social relationships and hence larger brains relative to their body size than all other animals

(2) Prediction 2: some primates will have more cognitively complex communication underpinning social relationships and hence larger brains than other primates

(3) Prediction 3: cognitively complex communication will be more effective than non-cognitively complex communication in mediating social relationships in complex social settings

(a) Vocalisations

- (b) Gestures
- (c) Complexity of structure
- (d) Perception
- (e) Intentionality
- (f) Referentiality
- (g) Laterality
- (h) Learning and innovation
- (i) Arousal control
- (j) Rewarding communication

(4) Prediction 4: greater social complexity will be associated with greater complexity of cognitive skills underpinning communication

- (a) Group size
- (b) Temporal and spatial stability of social system
- (c) Group density
- (d) Member roles
- (e) Despotic and egalitarian structure
- (f) Mating system
- (g) Bondedness style

IV. A brief review of evidence for communicative roots of complex sociality and cognition

V. Using social network analysis to examine the link between communication, cognition and sociality

VI. Conclusions

VII. Acknowledgements

VIII. References

IX. Supporting information

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 *et al.*, 2008; Barton, 1996; Byrne & Whiten, 1989; Clutton-Brock & Harvey, 1980; Dunbar, 1992, 1998; Evans *et al.*, 2005; Finlay, Darlington & Nicastro, 2001; Gibson, 1986; Harvey, Clutton-Brock & Mace, 1980; Hofman, 1983; MacLean *et al.*, 2014; Miller, 1999; Moll & Tomasello, 2007; Reader & Laland, 2002; Van Schaik, Isler & Burkart, 2012). The comparative method has been used as a powerful tool that has enabled scientists to increase our understanding of how the pressures of the socio-ecological environment have influenced 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 explains relative brain size variation in non-human primates (hereafter primates), because it is cognitively demanding as it requires that individuals learn flexibly from others and invent new behaviours. This cognitive capacity enables primates to exploit their environment in new ways and so exposes them to advantages of novel selection pressures (Lefebvre *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 correlates 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 the 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 the 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 & Corp (2004) showed how the frequency of tactical deception correlates with neocortex volume in primates, suggesting that strategies of social manoeuvring have driven the evolution of larger brains in socially complex species. However, it has been argued that tactical deception derives from life in complex social groups and therefore it cannot drive brain size evolution. Moreover, competition and exploitation are detrimental to social cohesion and thus social strategies that enable large social groups to function cohesively may be important in explaining complex cognitive skills and large brains in primates (Dunbar & Shultz, 2017).

These social explanations have been complemented 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). Early studies showed that primates with more complex frugivorous diets have larger brains than folivorous species. Fruit is more widely distributed across time and space as compared to folivorous foods. Mentally tracking and finding the location of scattered and unpredictable foods is cognitively demanding and therefore primate species exhibiting greater dietary complexity are hypothesised to have larger brains than species exhibiting lower dietary complexity (DeCasien, Williams & Higham, 2017; MacLean *et al.*, 2014). These new hypotheses have reignited the debate over which factors 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

encephalisation and the complexity of the social system (Broad, Curley & Keverne, 2006; Curley & Keverne, 2005). The highest rates of encephalisation can be found in the Primates but also other mammalian suborders such as Hippomorpha (horses), Tylopoda (camels), Odontoceti (toothed whales) and the Caniniformia (dogs and seals) (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 with neocortex size in relation to the rest of the brain (the neocortex ratio). Thus in many non-primate species, a pair-bonded mating system rather than group size is associated with larger brain size (Shultz & Dunbar, 2007). By contrast, in primates there is a strong relationship between group size and brain size (Dunbar & Shultz, 2017). 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 encephalisation in primate species, as compared to other mammals (Broad *et al.*, 2006; Shultz & Dunbar, 2007). The social brain hypothesis proposes that the social world of primates is particularly cognitively demanding and that this led to the evolution of increasingly large brains. The social brain hypothesis is specifically about the selection pressures arising from the need to create a functional, bonded social group, with sociality itself driven by the need to solve the ecological challenge of predation (Dunbar & Shultz, 2007, 2017). However, there is a lack of studies examining how this social complexity could 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 in 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. Group size is an emergent property of the ability of primates to maintain and coordinate social relationships and is used as an indicator of the complexity of social groups, as it is one of the 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.

The social brain hypothesis (as opposed to the Machiavellian version) is focused specifically on the need to manage social relationships in order to create functional and cohesive social groups (Dunbar, 1998). Studies linking social complexity and cognition should thus 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 characterise 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). In addition, primates with larger neocortices differ from other mammals in having bonded

relationships (Dunbar & Shultz, 2007). Although these 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 encephalised compared to other mammalian species, or why the relationship between encephalisation and group size is stronger in primates than in 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 blue wildebeest, *Connochaetes taurinus*) live in social groups but these groups are just loose aggregations, without stable membership or relationships among individuals ('non-bonded social systems'). By contrast, primates live in groups with stable membership, where they form long-lasting and differentiated bonds with unrelated conspecifics ('bonded social systems'). 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 high costs of competition for resources such as food and mates resulting from living in close proximity tends to drive animals apart, giving rise to the loose aggregations of many mammal species (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) as well as reduced female fertility (Dunbar & Mac Carron, 2019; Dunbar, Mac Carron & Shultz, 2018). The key mechanism used to create social bonds in primates is grooming as this releases endorphins, reducing stress in the recipient. Although there is an inherent difficulty in defining what a social bond is in non-verbal animals, given it is experienced (or felt), there is a consensus that without grooming reciprocity, it is not a

bonded relationship. As a functional outcome of these social bonds, dyad partners engage in a variety of coordinated interactions such as mutual grooming, mutual visual contact, joint travel and proximity (Dunbar & Shultz, 2010). The nature of the social setting within which dyads interact may increase the cognitive demands behind the formation and maintenance of bonded relationships through grooming. Primates may form social bonds in less-complex social settings (e.g. smaller groups, stable groups, low-density groups, despotic social organisation, monogamous species) or in more complex social settings (e.g. larger groups, fission–fusion, high density, egalitarian, polygamous). As well as grooming, communication is a crucial way to coordinate and regulate social bonds in primate societies, but the role of communication in social bonding has received limited attention, despite its potential significance for furthering our understanding of how the complexity of cognitive skills is related to the complexity of sociality (Fig. 1). Communication is defined as 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. By contrast, cognitively complex communication employs signal flexibly, which implies that signallers have voluntary control over communication (Tomasello & Zuberbühler, 2002).

The purpose of this review is to explore the cognitive complexity in communication that may have led to the emergence of complex social systems in primates. Here we strictly consider complex social systems as those where species form stable, bonded social relationships with unrelated individuals (Dunbar & Shultz, 2017). Social bonds of primates are associated with different patterns of communication through the intensity of emotional

arousal, whereby individuals express their own emotional arousal and also evaluate and process emotional arousal in others, in order to respond adaptively (Clay & de Waal, 2013; Eisenberg & Fabes, 2006). 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 *et al.*, 2013; Thompson *et al.*, 2010) or nasal temperature (Kano *et al.*, 2016). Arousal change is associated with corresponding changes in communication patterns, classified along the dimension of intensity or strength such as the potency of its presentation (loudness), frequency and duration (Burgoon *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 *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 *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 *et al.*, 1998). By contrast, low-arousal signals can have a stress-buffering effect on the recipient. Thus, low-intensity signals are particularly adaptive in frequent one-on-one interactions due to lower stresses incurred by the interaction, and this adaptive value of low-intensity signals can facilitate social bonding activities and proximity (Nakayama *et al.*, 2005; A.I. Roberts & Roberts, 2016).

By definition, communication in any primate species has evolved to influence the accuracy and speed of responsiveness by the recipient (Chittka, Skorupski & Raine, 2009).

The intensity of the arousal state in communication has recently been raised as an important aspect of social bonding because it influences the efficiency by which the recipients can infer the goal of the signaller and thus respond adaptively. In primates, forming bonded relationships appears to be particularly cognitively demanding, because signallers direct the recipient's movement and attention towards joint goals by means of low-intensity communication, whereas the recipient recognises and memorises the link between the communication and the goal (referent) of signalling in order to respond accurately. However, low-intensity signals (e.g. manual, visual gestures) may contain unspecific information about the referent (goal) of signalling and require rich contextual information to interpret them (Engh *et al.*, 2006). For instance, when a female indicates her desire for an infant to climb onto her back for travel, she may make an abrupt manual movement executed from towards to behind her body ('Backward sweep'; Video S1). If the infant is not acquainted with the gesture, it may be unclear whether the female is indicating her desire for the infant to climb onto her back to travel, or an alternative, such as her desire for the infant to cling to her chest for travel. Thus, when the link between morphology (e.g. abrupt manual movement executed from towards to behind the female's body) and the referent (e.g. the female's back to be climbed for travel) is not known in advance, the recipient may use contextual perception to respond adaptively (Noordzij *et al.*, 2009). In this type of perception, the recipient makes the link between the signal and the referent by using the identity of the signaller, the past relationship between the signaller and the recipient, and the ongoing context (e.g. mating, aggression, travel).

In circumstances when the communication takes place in complex social settings, which include other conspecifics than just the signaller and recipient dyad, this complexity can reduce contextual perception 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 unpredictable social partners such as same-age partners with whom dominance relationships are unresolved (Aureli, 1997; Schino *et al.*, 1988; Roberts, Chakrabarti & Roberts, 2019a; Roberts, Murray & Roberts, 2019b). These partners may influence the level of anxiety experienced by the social partner. As anxiety increases, it may be more difficult for the recipient to access their knowledge and infer the referent from the behaviour, leading to reduced coordination of social bonding (Sonnenschein, 1986). A whole range of behaviours are affected by the presence of a competitive audience and make contextual perception of low-intensity signals less effective in social coordination, including joint attention and close proximity between signaller and recipient, as well as the recipient's visual monitoring of the communication channel. Here we argue that as the complexity of the social setting increases, there will be an asymptotic limit on contextual perception of low-intensity signals. This limit will lead to the evolution of informative communication that, although cognitively complex from the perspective of the signaller, reduces the demands on contextual perception, by locating the referent in time and space for the recipient, to enable more effective formation of social bonds (Fig. 2) (A.I. Roberts & Roberts, 2016; Cullen, 1966, Marler, 1961). Thus, in order for the communication to be successful in conveying the signaller's goal, when social complexity increases there will be selection for greater cognitive skills that increase the effectiveness of communication in social bonding. These skills include a greater ability of the signaller to understand the recipient's comprehension state and respond to this knowledge by increasing information content in the signal (e.g. through structural complexity, intentionality, attention-getting, referentiality, innovation, and manual precision) (Roberts, Roberts & Vick, 2014a).

Informative communication is characterised by a greater ease of making an association between the referent and the morphology of the signal by the recipient, as compared to non-informative signalling. In informative signalling, attention is drawn to the

physical space/object or event towards which the recipient should act. This type of signalling reduces uncertainty by increasing the number of information units that recipient can use – in turn, this reduces the number of action opportunities the recipient needs to consider in deciding how to respond. For instance, if the infant does not respond to the ‘backward sweep’ gesture by climbing onto the female’s back, she may subsequently lower her back downwards or sideways in addition to making the ‘backward sweep’ gesture, in order to indicate the place where the infant should climb for travel. Thus, in this act of elaboration, the ‘backward sweep’ gesture is spatially linked to the referent to which it refers (the exposed back that needs to be mounted for travel), thereby reducing the infant’s need to contextually infer the referent among a set of potential action opportunities. As the social complexity increases further, the reduction in the costs of contextual perception of low-intensity communication through informative communication may also reach an asymptotic limit, where further increases in the informative value of low-intensity signals will have no bearing on the effectiveness of social interactions. As a result, the power of 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, complex signal is unsuccessful. Classical ethologists proposed that one important way to make signals more effective in eliciting an appropriate response from the recipient is by exaggeration of intensity or amplitude (Blute, 2006). For instance, the signaller might use a loud vocalisation simply to get its message across, even if the signaller and receiver are separated by a short distance. The grooming interaction may be mediated by use of a mechanically effective but gentle tactile gesture simply to make the message more transparent to the recipient, even if the signaller and receiver are both visually attentive. Increasing the amplitude of signals fulfils an important role in mediating social interactions when social attention is distracted, because high-intensity

signals tend to be more specific to the ongoing context and trigger a set of neural and physiological responses in the recipient that lead to an appropriate response from the set of potential action opportunities, therefore reducing the need to infer the goal of the signaller from the context. For instance, in the example of the female initiating travel with the infant given above, one would expect that the female would communicate by lowering her back downwards or sideways as well as using her hand in the shape of the 'backward sweep' gesture to exert force on the infant's body so as to cause the infant to move towards the back. By being physically displaced by movement/shape of the hand in the direction of the referent/spot on the body in the presence of the presentation of the referent/spot on the body, the recipient can make the link between the movement/shape of the hand and the referent. Thus, this type of signalling eases the recipient's comprehension of the signaller's goal by making the link between the gesture and the referent less ambiguous and more apparent (Fig. 3).

Although this strategy opens the way to increasing the efficiency of signals in conveying the signaller's goals, on a regular one-to-one basis it may lead to separation between partners, as the recipient might avoid behaviour that is maladaptive if used on regular basis (e.g. causing overstimulation and thus increasing the recipient's stress levels or anxiety when being frequently exposed to it). A further, previously unexplored way in which the signaller can influence the receiver is by increasing the reward value of communication. We will discuss in more detail in Section II how some signals have specific properties that can stimulate the reward system of the recipient. Light and sweeping but mechanically ineffective touch can stimulate the sense organs and reward centres in the brains of the recipient particularly strongly. Similarly, synchronised, high-amplitude, rhythmical vocalisations appear to be particularly stimulating for group-living primates. By reducing the recipient's anxiety, the 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 signals can influence the recipient's accuracy of responsiveness by increasing the mental capacity of the recipient to infer the referent from the ongoing context through the action of social neurohormones (Domes *et al.*, 2007; Gruber *et al.*, 2016). For instance, when initiating travel, a female can couple the hand shape of the 'backward sweep' gesture with gentle sweeping contact with recipient's body in the presence of lower back presentation. In this case, receiving rewarding stimulation in the presence of movement/shape of the hand and the presentation of the referent/spot on the body may facilitate making the link between movement/shape of the hand and the referent by the recipient. Thus, these rewarding features of communication can have a particularly powerful effect, such that the social cohesion of the group can be preserved in the 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 a particularly important role in social evolution.

From this it follows that socially complex primate species must solve problems relating to the formation and maintenance of bonded relationships using cognitively complex communication. Primates must be able to employ communication flexibly and adjust their communication according to the comprehension of the recipient. This adjustment requires complex understanding of other comprehension states, contingent on the tracking of social relationships and the memory of past interactions, rather than moment-by-moment adjustments to the current behaviour. It demands an understanding of intentionality, as to communicate effectively the signaller has an understanding that the direct social relationship (that based on the strength of the social bond 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 comprehension. This is equivalent to mentally modelling outcomes of different behavioural strategies that signallers can use towards the recipient and flexibly choosing one communication strategy over another to ensure that this communication strategy is effective in influencing the recipient. Thus, the reduced reliance on olfactory and hormonal determinants of affiliation in primates (Broad *et al.*, 2006) would have been coupled with the increased importance of cognitively complex communication that is necessitated by living in complex social groups, in order to develop and maintain long-lasting social bonds with unrelated group members.

This illustrates the central point that we make herein that there is a greater need to form and maintain bonded social relationships through cognitively complex communication in socially complex primate species, as compared to socially non-complex species. In complex social settings, conspecifics can develop and maintain bonded relationships through cognitively complex communication more effectively than through less cognitively complex communication. Thus, the evolution of cognitive skills underpinning communication in primates in order to meet the challenges of bondedness in complex social settings may have been a key innovation that facilitated the emergence of complex social systems (Dunbar & Shultz, 2017; Roberts *et al.*, 2014a, 2012b). Here we propose that cognitive demands behind the communication needed to form and maintain bonded social relationships in complex social settings drive the link between brain size and sociality. To test this hypothesis, we propose the following set of predictions: (1) primates will have more cognitively complex communication underpinning social relationships and hence larger brains relative to their body size than all other animals; (2) some primates will have more cognitively complex communication underpinning social relationships and hence larger brains than other primates; (3) cognitively complex communication will be more effective than non-cognitively complex communication in mediating social relationships in complex social settings; (4) greater social

complexity will be associated with greater complexity of cognitive skills underpinning communication. In Section II we discuss historical perspectives leading to this hypothesis. Section III sketches out details of communication innovations that may have enabled the kinds of bonded social relationships in complex social settings that we find in primates (summarised in Tables 1 and 2). In Section IV we briefly outline some of the empirical evidence from primate studies in support of the hypothesis. Finally, in Section V we describe how the study of communicative roots of socio-cognitive skills can be enhanced by use of social network analysis.

II. HISTORICAL APPROACH

Jean-Baptise Lamarck and Charles Darwin were pioneers in linking 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 (1809/1963, p. 172) 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”. Following from this argument, Darwin (1872/1965) 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 great importance for maintaining social relationships in social animals. In the twentieth century, Marler (1977, p.46) was amongst the strongest advocates of the link between social and communicative complexity, noting: “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 favours specialized ‘information-transfer’ abilities, depend[s] on the social system”. In recent years, this debate was extended by Maestripieri (1999, p. 56) who 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, encephalization, 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; S.G.B. Roberts & Roberts, 2016; 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” (Freeberg *et al.*, 2012, p. 1787). We now 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

(1) Prediction 1: primates will have more cognitively complex communication underpinning social relationships and hence larger brains relative to their body size than all other animals

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 result 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 *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 & Keverne, 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 the 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). Since social bonding is flexible it may be expected that cognitively complex communication will be necessary to facilitate bondedness and this will give rise to larger brains in primates than in other species.

(2) Prediction 2: some primates will have more cognitively complex communication underpinning social relationships and hence larger brains than other primates

The social characteristics of primate groups differ across a number of dimensions, perhaps the most important of which is the degree of influence of kinship on intraspecific social dynamics. In many primate species, the 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 (Maestriperi, 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 reduction in hormonal priming for affiliative behaviour demands more complex communication skills. In these societies, complex communication facilitates the formation and maintenance of social bonds with unrelated and less-familiar conspecifics and this has an influence on individual success in the group and fitness (Maestriperi, 1999). Hence the cognitive skills underpinning communication and social bonding will be greater in those primate species where social relationships are less influenced by kinship.

(3) Prediction 3: cognitively complex communication will be more effective than non-cognitively complex communication in mediating social relationships in complex social settings

(a) Vocalisations

The referential ability underlying vocalisations suggests that important aspects of primate cognitive abilities related to sociality are present in calls. Primates have complex cognitive abilities in the vocal domain indicated by functionally referential calls that can reliably provide recipients with information about the presence of predators or food in the environment (Zuberbuhler, 2009). For instance, vervet monkeys (*Chlorocebus pygerythrus*) 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, Cheney & Marler, 1980). Chimpanzees in captivity produce acoustically different food grunts in response to quality of the food eaten (Slocombe & Zuberbuhler, 2005, 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, Gouzoules & Marler (1984) showed that rhesus macaques (*Macaca mulatta*) produce acoustically different scream variants as a function of aggression severity, relatedness and 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 *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, *Pan troglodytes*, 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 the vocal domain may be

more constrained. Although primates can modify existing call types to match those of the partner (Watson *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 macaques and Japanese macaques (*Macaca fuscata*) produces no significant changes in the repertoire or structure of their species-typical vocalisations (Owren *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 difficulties in the communicative mechanism controlling vocal output (Lieberman, 1968). Whilst the basic vocal tract anatomy of primates would support production of complex sounds, 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 primates as compared to humans (Jurgens, 1998).

Despite these limitations of cognitive skills in the vocal domain (Fischer, 2017) other results demonstrate the importance of vocalisations in sociality. The notable example of this 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 the evolution of a large vocal repertoire and brain size. Another exception is the evidence that chimpanzees direct lower intensity calls towards bonded social partners (S.G.B. Roberts & Roberts, 2019). Use of visual gestures combined with low-intensity calls occurs at a higher rate between individuals who spend longer periods of time in proximity.

(b) *Gestures*

There is a number of theoretical and empirical studies indicating that the gestural modality of communication is more important in facilitating social complexity than vocalisations (Burling, 1993; Corballis, 2003; Dunbar, 2012; Hewes, 1992, Roberts *et al.*, 2012*b*). This is because primates have 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 *et al.*, 1999) and in captivity (Tomasello *et al.*, 1985). Additionally, whilst primates display an inability to learn vocal modifications, they have the 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 some evidence of intentionality in primate calls], whereas they have the ability to use gestures intentionally in their interactions both with humans (Cartmill & Byrne, 2007; Leavens, Russell & Hopkins, 2005; Roberts *et al.*, 2014*b*) and with conspecifics (Roberts, Vick & Buchanan-Smith, 2012*a*, 2013).

When exploring the link between cognitive skills underlying gestural communication and sociality, empirical studies of manual gestures (defined as communicative movements of hands) suggest that manual gestures play a key role in sociality (Roberts *et al.*, 2013). In particular, manual gestures without using or touching objects or the substrate (brachiomanual gestures) are important (Pollick & de Waal, 2007). 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 area 44, which is homologous with the human Broca's area, is enlarged in the left hemisphere (Cantalupo & Hopkins, 2001). In contrast to vocalisations, the monkey's Brodmann area is activated during both the production and perception of manual movements (Rizzolatti *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 *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), demonstrating the importance of manual gestures in facilitating complex sociality (Roberts *et al.*, 2014a, 2012b).

(c) Complexity of structure

There is a large amount of variation observed in the complexity of communication signals both across and within primate species and this complex communication (e.g. combinations, multimodal) may facilitate increases in social complexity. Communication signals can occur on their own, or they can be accompanied by the use of other signals, visual orientation or objects (see online Supporting Information, Video S1). Signals produced by the signaller can be homogenous and therefore occur in the repertoire of both the signaller and the recipient, or these signals can be heterogeneous, where the signal occurs in the repertoire of the signaller, 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, which in turn influences the efficiency with which the recipient can respond to communication (Dawkins & Guildford, 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 the premotor cortex, enabling the recipient to evaluate more consciously the expectation of signaller's intent than gained from processing of facial expression alone (Conty *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. This indicates that complex communication could play an important role in regulating social interactions in complex social systems, where different types of signalling have different but complementary functions.

There are however, many different ways in which the signaller can achieve a greater efficiency of communication through the complexity of their signalling in complex social settings. The complexity of 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. This 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 when social complexity increases as compared to discrete signalling. Whereas in many mammal species, distinctive signals are inflexible and genetically determined, in primates many distinctive signals are flexibly produced. Production of these signals requires flexibility because these signals only loosely originate from pre-existing morphological forms. Thus, greater complexity of communicative structure (i.e. flexibly produced graded and distinctive repertoires) may be important sources of information in socially complex species.

(d) Perception

The ability to perceive communication is a critical aspect of social interactions (Seyfarth & Cheney, 2013). The overall structure of communication can influence 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 *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. By contrast, for graded communication, a greater variety of signal types and forms are used in relation to specific goals or intentions. As compared to discrete signals, 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 (Leavens *et al.*, 2004; Pollick & de Waal, 2007). Thus, the perception of graded signals in primates could be constrained and there will be an upper limit to the number of relationships that individual primates can maintain through these signals. If the number of individuals in a group becomes too large, it may become more

difficult for individuals to interact through graded signals with all group members. Given the greater processing demands of graded communication, there may be a greater capacity for perception of these signals in species that maintain complex social groups.

(e) Intentionality

Intentionality is another characteristic of communicative complexity that may enable primates to coordinate behaviour effectively in complex social settings. 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 *et al.*, 1985). Intentional communication may be operationalised in the form of goal persistence, response waiting or sensitivity of the signaller to the recipient's attentional state when producing acts of communication. 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. the recipient changing their behaviour from grooming to travel) (Golinkoff, 1986, 1993). Such communication shows the ability of the signaller to understand that the recipient is an intentional being with a comprehension state which may differ from their own, but which can be altered by communicative behaviour (Tomasello, Hare & Fogleman, 2001). Intentionality in communication is indicated by persistence, where 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). For instance, if the recipient is not responding in the manner that matches the goal of the signaller during a grooming initiation, or the response is incorrect, the signaller can use another gesture to elicit grooming. Communicative persistence can thus improve the efficiency of social bonding between two individuals because it increases the likelihood that the recipient will understand

more accurately 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.

(f) Referentiality

Another key function of communication that would facilitate social bonding alongside increases in social complexity is the ability of the signaller to influence the behaviour of the recipient by directing their movement and attention towards either the self (reference to the signaller), other (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 *et al.*, 1980). In instances of referential signalling, there is 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, Tagliatela & Leavens, 2007; Leavens *et al.*, 2004; Roberts *et al.*, 2014a,b). Furthermore, primates can draw the attention and movement of the recipient to the recipient themselves, by the use of directional manual gestures. 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 gesture could be viewed as having characteristics of referential signalling (e.g. 'limp extend', see video clip at www.youtube.com/watch?v=Ut3Gu9Eoqjk; Roberts *et al.*, 2014a,b). Camaioni (1993) argued that this type of visual gesturing may have

greater cognitive complexity than either tactile (received through tactile sensation) or auditory (received through hearing) gestures. Visual gestures demand that the signaller sees the recipient as capable of comprehension that the interaction can be causally influenced by distal means. By contrast, tactile or auditory gestures may exercise a direct causal effect on the recipient that may be 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 the referential nature of this type of signalling (Roberts *et al.*, 2013). Thus, this capacity to refer to entities external to the self can increase the efficiency of social coordination by increasing the ability of the recipient to identify the goals of the signaller regarding changes in the recipient's behaviour (S.G.B. Roberts & Roberts, 2019).

(g) *Laterality*

The ability to coordinate social relationships in primates in order for the complex group to function as a cohesive whole (Dunbar & Shultz, 2017), may be influenced by laterality defined as dominance of one side of the brain in controlling particular activities or behaviours (Fitch & Braccini, 2013). An important distinction between the left and right hemispheres (and hence opposite perceptual fields) is that the right brain processes the emotional content/relevance of signals faster than the left side does. As a result, animals may approach, watch each other or fight with the opponent preferentially in the left visual field (Casperd & Dunbar, 1996). There is a widely documented hemispheric bias in the use of primate manual gestures, where left-handed gestures are controlled through the right hemisphere and right-handed gestures are controlled through the left hemisphere. In humans, right-hemisphere-controlled manual gestures are more emotionally expressive than left-hemisphere-controlled manual gestures (Sackeim, Gur & Saucy, 1978). Left-handed gestures

can lead to attentional and behavioural convergence by inducing compatible affect between two interacting individuals (Owren & Rendall, 2001). By contrast, right-handed gestures can increase the perceptual salience of referents, in order to draw the recipient's attention (Roberts *et al.*, 2019b). For instance, in humans, right-handed gestures are more effective in accurately pointing out the target of communication than left-handed gestures. By increasing the accuracy of manual indication (Mutha, Sainburg & Haaland, 2010), right-handed gestures can spatially disambiguate a referent among a set of potential targets and coordinate social interactions more effectively. For instance, in contexts of antagonism, recruitment of support from bonded social partners may depend on the ability of the signaller to indicate to the recipient precisely that they are the target of a gesture (Video S2). Further, right-handed gestures made in the context of grooming can spatially disambiguate to the recipient which body part they should move, and this would aid the efficiency of establishing social bonds with the recipient by reducing the risk of miscomprehension. The capacity to coordinate movement and attention through increased precision of manual indication by use of right-handed gestures is one characteristic of the complex cognitive skills that may lead to increased social complexity, by improving the ability of the recipient to respond accurately to communication (Roberts *et al.*, 2019b). For instance, 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.

(h) Learning and innovation

Communication innovation (creating new signals) and communication learning (copying or modification) are two complementary processes that may facilitate social bonding when social complexity increases. 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 *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 distinct patterns in the overlap of communicative repertoires, with both homogeneity (presence of the same signal in the repertoire of both signaller and recipient) and heterogeneity (presence of the signal in the repertoire of the signaller but not in the repertoire of the recipient) occurring within dyads. Many different hypotheses have been proposed to explain patterns of homogeneity in the repertoire of gestures in primates [see Liebal, Schneider & Errson-Lembeck (2018) for a review]. Building on studies of gesture acquisition in humans, we propose that homogeneity in repertoire occurs as a result of learning by recipients over repeated instances of dyadic interactions in which they assign a specific referent to heterogeneous gesture forms (Roberts *et al.*, 2019b; Roberts & Roberts, 2017). For instance, a female chimpanzee may sweep her arm backwards towards the infant whilst simultaneously lowering her back to indicate desire to travel. Backward sweep can over time reliably predict lowering of the back and hence desire to travel (Video S1). Over repeated instances of these interactions, backward sweep may become associated with the desire to travel when lowering of the back is absent (see e.g. Video ‘backward sweep’, <https://www.youtube.com/watch?v=GPLaw032j7o>). In this way manual visual gestures (backward sweep) are derived from mechanically effective but gentle tactile gestures (physically sweeping the infant onto the lowered back). In this case, the infant first makes a link between the shape and movement of the hand/arm and referent (lowered back) in a tactile domain, and transfers this association to a visual domain (the shape and movement of the hand/arm executed without tactile contact in the presence of a lowered back). Over time dyad partners move away from salient gestures (e.g. ‘backwards sweep’ and ‘lowering back’ together) and towards less salient gesturing (e.g. ‘backwards sweep’ only) (see Fig. 3). The

overlap (homogeneity) of repertoire arises as the gesture/referent link becomes gradually integrated in the memory of the recipient in instances of repeated dyadic interactions. Making this link causes automatic mapping between the signal and the referent each time the signal is reproduced and observed, thus reducing cognitive demands on contextual perception. For instance, signals can encode the space towards which to act and the space subsequently becomes referenced in an emotional signal that is only intelligible and referent specific between partners with a history of prior interaction. Thus, homogenous repertoires are a product of social-bond formation that are highly efficient in coordination between dyads with overlapping interests (Dawkins & Guilford, 1997; Wittgenstein, 1953).

On the other hand, where social complexity increases, these same patterns of gesturing directed at bonded social partners may become less effective when directed at partners with whom social bonds are weaker. Although heterogeneous communication contains attention-getting properties that increase the likelihood that the recipient will pay attention to the signaller (Cullen, 1966, Marler, 1961), there is evidence in chimpanzees that single heterogeneous gestures are less likely to receive a response from a partner (Roberts & Roberts, 2017). Further, in humans heterogeneous communication demands greater skills of contextual perception to process (Noordzij *et al.*, 2009). As a result, recipient may experience difficulty in accessing their knowledge and inferring the signaller's referent from the history of past interactions. This may lead to overgeneralisation of the referent and miscomprehension between partners, which in turn may lead to reduced opportunities for social bonding. Thus, when social complexity increases, signallers may use informative communication to increase the recipient's knowledge of the referent of the gesture and hence increase likelihood that they will respond (Nakayama *et al.*, 2005; A.I. Roberts & Roberts, 2016). For instance, as the signaller clarifies its referent, in repeated instances of miscomprehension, the link between the referent and signal is shaped from the signaller's

pattern of repetition and elaboration in relation to the recipient's behaviour towards the referent. If the recipient shows complete miscomprehension (e.g. lack of response to the initial gesture), the signaller elaborates through communication means that refer to the role of the recipient in the interaction (e.g. using a tactile gesture to move an infant's body towards the female back to climb for travel). If the recipient shows partial miscomprehension (e.g. approaches half-way), the signaller repeats the initial gesture (Roberts *et al.*, 2013). In addition, rewarding features of signalling (e.g. mutual visual contact accompanying use of signals, light sweeping touch, soft vocal and non-vocal sounds, high intensity synchronized calls) can also increase the ability of the recipient to recognise and learn gesture–referent links (Gruber *et al.*, 2016). As the rewarding value of the communication increases, it is more likely to be responded to by the recipient, in turn leading to more effective social bonding. This process leads to a positive feedback loop whereby opportunities for learning and social-bond formation in complex social settings originate in the need to reduce cognitive demands on contextual perception through informative and rewarding communication (Fig. 4).

(i) Arousal control

Flexibility in modifying arousal underpinning communication may be important to regulating social relationships in socially complex species, but such flexibility requires greater cognitive skills than the use of a simpler communication system in an inflexible way (Liebal & Oña, 2018; S.G.B. Roberts & Roberts, 2016). Voluntary control underpinning communication is seen when signallers suppress their pre-potent drive to express high emotional arousal through high-intensity communication and instead use low-intensity signals to communicate (Tops & Boksem, 2011). The ability to inhibit pre-potent responses correlates with prefrontal cortex volume and depends on 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 circumstances when the dominance relationships have been unresolved, as is often the case in more egalitarian, bonded species (Maestriperi, 1999). Thus, by reducing the arousal associated with communication, signallers can be more successful in eliciting a response from the signaller without resorting to the 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 complex social settings. This ability to control high-intensity arousal may be particularly evident when stopping and pausing high-intensity communication acts to prevent overstimulation of the recipient and therefore increase opportunities for social bonding.

(j) Rewarding communication

In primates, rewarding communication may play a particularly important role in mediating social relationships when social complexity increases. This type of communication may create a psychopharmacological environment that enhances the recipient's commitment and attention to the social interaction by reducing their stress. For instance, a mild sweeping touch as well as more intense tactile contact (Video S3) can act as a stimulus that has the potential to activate neural sensory afferent fibres (C fibres) involved in the release of a suite of neurohormones that act on the reward system.

Further, high-intensity, synchronised vocalisations accompanied by loud, rhythmic, auditory gestures such as drumming (Video S4) 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). Through increasing pleasure from the interaction, rewarding communication can facilitate comprehension when the dyad partners have weaker social bonds and therefore the recipient is not willing to respond to communication. In this case, rewarding features of communication can facilitate making of the link between the referent and the signal more effectively than when the communication does not contain the rewarding features in the signalling.

(4) Prediction 4: greater social complexity will be associated with greater complexity of cognitive skills underpinning communication

(a) 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, functionally cohesive units (Dunbar & Shultz, 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 due to the demands imposed by the requirement to monitor a more dynamic and complex social

environment. 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. Further, primates must be able to use different communication strategies and behaviours flexibly to maintain ties of different strength. Finally, it could be predicted that the structuring of the group may change, with an increasing number of sub-groups forming in larger groups.

(b) 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 activity (e.g. resting, feeding) and distribution of resources (Aureli *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). By 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).

In a fission–fusion social system, the cognitive demands behind monitoring social relationships based on irregular interaction may cause primates to experience greater distraction resulting in weaker social bonds than in stable social systems (Barrett *et al.*, 2003). Thus in a fission–fusion social system, there may be a greater need for flexibility in communication through the use of differentiated communication strategies relative to a stable social system.

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 fission–fusion species will result in animals having to keep track of more indirect relationships with whom interactions may be infrequent (Barrett *et al.*, 2003). Thus, the influence of group size on the patterning of social relationships and communication should be greater in fission–fusion than stable groups, as there are more differentiated social relationships in fission–fusion compared to stable social systems.

(c) Group density

Group density refers to the number of individuals per square kilometre who are members of the same social unit (e.g. the same group). In denser groups, where the number of individuals

who are in direct close proximity and direct social interaction is greater than in less-dense groups, the number of third-party social relationships in the immediate audience that individuals must track increases (Dunbar & Shultz, 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 (S.G.B. Roberts & Roberts, 2016). 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.

(d) 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). The role individuals play in the network will influence the complexity of the social setting within which they interact, and hence the cognitive demands of recalling information about individual identity of social partners in different social roles and in different contexts (Conty & Grèzes, 2012; Roberts & Roberts,

2017; S.G.B. Roberts & Roberts, 2019). For instance, when the risk of mortality or injury is high, some males may adopt the role of dominant ‘protector’ males of vulnerable individuals who may stay in closer proximity to them (Altmann, 1979; DeVore & Washburn, 1963; Hockings, Anderson & Matsuzawa, 2006; Otali & Gilchrist, 2006; Reynolds, 1963). When individuals play many different roles in the network, there may be greater difficulty involved in the formation and maintenance of social bonds and hence a greater need for more flexible communication.

(e) Despotic and 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 antagonises the subordinate individual over access to resources but is never supplanted or antagonised by the subordinate; and (2) egalitarian social relationships where the dominance relationships are more unresolved and thus social partners are equally likely to supplant or antagonise social partners (Goodall, 1986). In egalitarian species, there is a greater need for primates to keep track of their own relationships with the third-party audience, as changes in these relationships could have implications for the likelihood that these conspecifics will engage in contests over access to resources (Ay, Flack & Krakauer, 2007; Flack *et al.*, 2006). The need to track social relationships with a third-party audience in egalitarian species will lead to a greater difficulty in focusing on a signaller and hence weaker social bonding, which will demand that there is greater cognitive and communicative complexity underpinning social bonding.

(f) Mating system

In some mammals, females form an enduring, life-long 'pair bond' with a mating partner. In other mammals, females may form a 'pair bond' for shorter time periods such as one reproductive season or just a few days during a single reproductive period (e.g. chimpanzees) (Goodall, 1986). In some taxa, 'pair bonds' 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 a simpler form of sociality in smaller social groups, pair-living in complex social groups and especially within polygamous or promiscuous societies may be more cognitively demanding. Within polygamous/promiscuous species such as chimpanzees, the cognitive demands behind maintaining pair bonds are high because of the distraction imposed by the presence of alternative mating opportunities (e.g. mating with dominant males), which would require greater cognitive skills underpinning communication with the pair-bond partner than maintaining pair bonds in simpler social settings.

(g) Bondedness style

Some socially and cognitively complex primates (e.g. great apes such as chimpanzees, gorillas and humans) are based on male bondedness, as females disperse, whereas others are based on female bondedness, as males disperse (e.g. baboon–macaque–guenon group) (Greenwood, 1980; Hill, Bentley & Dunbar, 2008; Kudo & Dunbar, 2001; Lehmann & Dunbar, 2009). Both males and females form equitable social bonds which require remembering previous experiences with the partner, and making decisions about how to compete based on small differences in resource-holding potential. Unlike in female-bonded groups, primates in male-bonded groups face greater cognitive challenges related to social bonding with unrelated conspecifics, such as the need to recognise bondedness in the absence

of a shared history of association with the mother. Managing these social relationships ineffectively may have negative fitness consequences, in terms of a high risk of injury or death as result of physical conflict. Male-bonded social systems may also demand a greater need for monitoring of third-party relationships due to the greater risks imposed by a third-party audience. In these societies, animals may experience greater distraction from social bonding with a partner and hence weaker social bonding. Thus, it would be predicted that in male-bonded species there would be greater skills of complex cognition underpinning communication to form and maintain bonded relationships when compared with female-bonded social systems.

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

Most of our knowledge about the link between sociality and primate communication comes from studies of gestural behaviour in chimpanzees, as this is the great ape species whose gestural communication has been studied most intensively (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 S.G.B. Roberts & Roberts (2016). They found that gestural communication is associated with the duration of time spent in proximity. These observations were later supplemented by observations of intentional use of gestures in relation to proximity (A.I. Roberts & Roberts, 2019a). Chimpanzees that spent longer periods of time in proximity used persistence sequences at a higher rate 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 *et al.*, 2019a). Further, chimpanzees who spent shorter periods of time in proximity appear to engage in rewarding communication more often than chimpanzees who spent longer periods of time in proximity (A.I. Roberts & Roberts, 2019a). Chimpanzees produce ‘synchronised high-intensity pant-hoots’ (Video S4) – a form of communication where loud auditory gestures (e.g. drumming made by hitting a tree trunk with the feet) are responded to by the joint vocal reaction of a wider audience (S.G.B. Roberts & Roberts, 2016). Chimpanzees also produce tactile gestures that can be responded to by turn-taking episodes of visual or tactile gestures (Video S3) (A.I. Roberts & Roberts, 2019a). Both of these communication types appear to occur between pairs of individuals that spent a short time duration in close proximity (A.I. Roberts & Roberts, 2019a; S.G.B. Roberts & Roberts, 2016). These behaviours are shown to reduce stress in recipients, 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 data source with regard to the link between social and communication complexity comes from examining the communicative underpinnings of bondedness, or the degree to which chimpanzees engage in social interactions directly. These data demonstrate that bonded relationships in larger parties are maintained through cognitively complex communication more effectively than through less cognitively complex signalling (Roberts, 2018). For instance, 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 the ability to learn and flexibly adjust

manual movement, enabling more effective comprehension and learning of communication by the recipient (Mutha, Haaland & Sainburg, 2012).

Right-handed gestures have been shown to play an important role in maintaining bonded relationships in complex social settings. The bonded social relationships in average parties (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 & Guilford, 1997). However, when the complexity of the social setting increases, monitoring of the 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. When the size of the party reaches 13 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 these types of relationships cannot be maintained in larger social parties, due to the 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 to 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 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 experimental studies of language-trained apes. In a task that required the use of communication to obtain hidden food that could not be obtained individually, language-trained chimpanzees using communicative persistence to correct experimenters' understanding about the 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 that primate species could live 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 debate as to the cognitive underpinnings of

this flexibility in communication, and the cognitive abilities of non-human primates in general. Some researchers claim that non-human primates, and particularly some great ape species, have the ability to understand mental states in others (Krupenye *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 & 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 receivers 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 studies that showed the 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 (*Pan paniscus*), human children (Krachun *et al.*, 2009)] and deception [capuchin monkeys, *Cebus capucinus* (Wheeler & Hammerschmidt, 2013)]. More broadly, Barrett, Henzi & Rendall (2007) suggest that much of primate behaviour is not based 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. 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, measuring and comparing social complexity across groups and species. Currently, there is a lack of such standardised measures of social complexity (Kappeler, 2019) and developing such a measure that can be applied across different species has been described as the ‘grail of social analysis’ (Whitehead, 2008, p. 20). One promising approach to developing such a measure is social network analysis, which provides a way quantitatively to describe the patterns of interactions in any social system and can be used to compare social structures both within and between species. A network models a system composed of individual nodes (in animal networks typically individuals) and the edges or ties between the nodes (in animal networks typically some aspect of the social relationship between the animals). In the last two decades, social network analysis has increasingly been used to study sociality in both primate (Kudo & Dunbar, 2001; Lehmann & Dunbar, 2009; Sueur *et al.*, 2011) and non-primate species (Farine & Whitehead, 2015; Krause, Lusseau & James, 2009; Kurvers *et al.*, 2014; Wey *et al.*, 2008).

Social network analysis may be particularly valuable in exploring the associations between communication, cognition and sociality in two key areas. First, network analysis can provide novel insights into the properties of social structure within and among 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, James & Krause, 2007; Wey *et al.*, 2008). For example, social network analysis has recently provided novel insights into the underlying social structure of western lowland gorillas (*Gorilla gorilla gorilla*)

(Morrison *et al.*, 2019), discovering a hierarchical social modularity in which the lower-level reproductive groups and solitary males are organised into higher-level social units, with a hierarchical scaling ratio similar to that found in other mammalian species (Hill *et al.*, 2008). The precise, quantitative description of the social structure of primate groups possible with social network analysis is an important first step in developing measures of social complexity (Whitehead, 2008) and in then relating that complexity to patterns of communication. One key unresolved issue in comparing networks of different sizes both within and among species is that measures of network structure such as network density (the proportion of all possible ties that are present) are strongly related to overall network size (Farine & Whitehead, 2015; Faust, 2006; Faust & Skvoretz, 2002). More sophisticated statistical techniques for analysing social network data, and standardised ways of collecting, processing and analysing network data across different species, are needed to enable meaningful comparisons across networks of different sizes (Farine & Whitehead, 2015).

Second, network analysis can provide insights into the range of behaviours animals use to build social relationships and regulate their social interactions. In complex social systems, animals interact in many different contexts and maintain a differentiated set of social relationships (Freeberg *et al.*, 2012). There is a lack of consensus as to how to measure the nature of social relationships animals maintain with others, both in the broader field (Dunbar & Shultz, 2010; Silk, Cheney & Seyfarth, 2013) and in network analysis (Farine & Whitehead, 2015). In primates, most networks are based on proximity (S.G.B. Roberts & Roberts, 2016; Schel *et al.*, 2013) and/or grooming (Koyama, Ronkainen & Aureli, 2017; Schel *et al.*, 2013), with more recent research using rates of communication as the basis for the network (A.I. Roberts & Roberts, 2016; S.G.B. Roberts & Roberts, 2016). These behaviours may have very different functions, with grooming used to build relationships (Dunbar, 2010; Keverne *et al.*, 1989; Schino, 2007), and communication used to coordinate

and regulate social interactions (Faraut *et al.*, 2019; Fedurek *et al.*, 2013, 2015; Mitani & Gros-Louis, 1998; A.I. Roberts & Roberts, 2016; S.G.B. Roberts & Roberts, 2016). By contrast, proximity can be seen as the functional outcome of a relationship (i.e. two animals with a strong social bond will tend to associate with each other), rather than a mechanism used to build relationships or coordinate social interactions.

One specific empirical question that can be addressed with social network analysis is the extent to which the networks formed by these different behaviours overlap. For example, Lehmann & Ross (2011) used social network analysis in wild baboons (*Papio anubis*) to examine the extent to which networks based on different social behaviours were similar to each other. Networks based on grooming showed little overlap with networks based on other social behaviours, such as displacement, presenting or aggression. However, individual baboons who were central in one behavioural network tended to be central in the other behavioural networks. Whilst this study revealed the complexity in the baboons' social environment across affiliative, agonistic and sexual behaviours, it did not examine communication networks. Comparing the networks formed by different types of communication (e.g. gestures, low-amplitude vocalisations, high-amplitude vocalisations) will provide new insights into how primates use different types of communication to coordinate and regulate a differentiated set of social relationships (A.I. Roberts & Roberts, 2016; S.G.B. Roberts & Roberts, 2016). 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 a differentiated set of social relationships, whereas in less-complex social systems individuals would use fewer types of behavioural interactions to manage their relationships. Thus the networks based on different behaviours will show less overlap in complex as compared to non-complex social systems.

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 (Grove, Pearce & Dunbar, 2012). One key feature of complex social relationships of hominins is communication and the social network approach can be used to examine language evolution. To date, the lack of ‘fossilisation’ of language prior to the arrival of writing has made it difficult to draw inferences about the presence and form of language in our hominid ancestors (Fitch, 2005). When exploring language evolution it is important to examine whether language evolved to increase effectiveness of locating referents in time and space, thereby reducing cognitive demands on contextual perception (Hauser, Chomsky & Fitch, 2002). The studies of great apes indicate that the origins of cognitive skills underpinning language are in manual gestures, as primates have limited ability to voluntarily direct movement and attention of the recipient towards external objects and events through vocalisations (Bohn, Call & Tomasello, 2019). When the earliest expansion of hominins from Africa to open, grassland habitats demanded larger group sizes to reduce mortality from predation (Prat, 2018), the challenges of social complexity may have precipitated evolution of voluntary control in vocal signals such as synchronized choruses combined with auditory gestures (Darwin, 1872/1965, Hillert, 2016). These signals are highly rewarding (A. I. Roberts & Roberts, 2019b) and can refer to objects and events in the external environment (Boesch, 1991; Clark & Wrangham, 1994; Kalan, Mundry & Boesch, 2015). Thus as the social complexity increased, language evolution may have transitioned from manual gestures to ‘protosong’ (Darwin, 1872/1965): loud, auditory gestures (e.g. clapping) combined with synchronised choruses (e.g.

<https://www.youtube.com/watch?v=-T8qJ9D1-g8>). 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 language evolution, and using this approach could 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 (Snijders *et al.*, 2017). The role of habitat in influencing social structure has not been explored using social network approaches. However, habitat can influence the ability of the recipient to engage in social bonding by increasing the costs of processing information in the signals. For example, factors such as background noise, illumination, wind, habitat density can cause a distraction or factors such as temperature can influence metabolic costs of the recipient, leaving fewer cognitive resources that can be directed to processing contextual information and learning of the signals. 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, and the role communication plays in these social networks, will provide an invaluable tool in ensuring a long-term future for our closest living relatives.

VI. 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 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–gatherers (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 form and maintain bonded social relationships in socially complex species is a key factor in explaining the link between social complexity and cognition. Specifically we propose that the evolution of cognitive complexity underpinning the production of signals is driven by the need to reduce the cognitive demands arising from the contextual perception of low-intensity signals in recipients. By making these signals more informative and rewarding, signallers increase the probability the recipient will produce the desired response. In particular, we emphasise that manual gesturing was a key innovation that may have facilitated the more complex social

systems of primates (Roberts *et al.*, 2014a, 2012b). We provide the first comprehensive review that explains why the complexity of cognitive skills underpinning communication is important for managing social relationships, relative to less-cognitively complex communication. We provide information about a set of recent advances that suggests that communication that facilitates bondedness (e.g. intentionality, referentiality) when social complexity increases and social bonds weaken (e.g. joint attention declines) enables primates to develop bonded social relationships in complex social settings (e.g. larger groups).

(4) We argue that there is an asymptotic limit on the extent to which contextual perception of low-intensity signals can be effective when social complexity increases, and this leads to evolution of differentiated social relationships, whereby informative and rewarding signals come into play in facilitating complex sociality (Roberts *et al.*, 2019b).

(5) To date there is no evidence on how the complexity of cognitive skills underlying communication varies as a function of social complexity at the level of the group or 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 the origins of language.

(6) To carry out both within- and among-species comparisons, we propose the 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 that 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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IX. SUPPLEMENTARY INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Video S1. Arm extension used to initiate an infant's climbing onto the female's back for travel.

Video S2. Stretched extend gesture made with right hand towards the dominant individual during an aggressive event.

Video S3. Chimpanzee using a mechanically ineffective tactile gesture for social bonding.

Video S4. Synchronised high-intensity pant-hoot with drumming.

Table 1. Complexity of cognitive skills underpinning communication and social complexity.

Cognitive complexity variable	Presence of communicative complexity within social relationships in:	
	Bonded social system	Non-bonded social system
Vocalisations	Present	Present
Gestures	Present	Absent
Complexity of structure	Present	Absent
Contextual perception	Present	Absent
Intentionality	Present	Absent
Referentiality	Present	Absent
Laterality	Present	Absent
Learning and innovation	Present	Absent
Arousal control	Present	Absent
Rewarding communication	Present	Absent

Table 2. Sources of recipient's distraction/anxiety according to social complexity.

Social complexity variable	Non-complex sociality	Complex sociality	Source of recipient's distraction/anxiety in complex social setting
Group size	Small	Large	Monitoring large number of social relationships
Temporal and spatial stability of social system	Stable	Fission–fusion	Monitoring social relationships based on irregular interactions as individuals encounter each other less often
Group density	Low	High	Tracking large number of third-party social relationships in the immediate audience
Member roles	Single role	Multiple roles	Monitoring social relationships across different functions and contexts
Despotic/egalitarian social system	Despotic	Egalitarian	Monitoring partners with whom dominance relationships have been unresolved
Mating system	Monogamous	Polygamous	Monitoring alternative mating partners such as dominant male
Bondedness style	Female bonded	Male bonded	Monitoring partners with whom kinship status has been unresolved

Fig. 1. Process of the formation and maintenance of social bonds. Top arrow indicates an increase in emotional closeness; bottom arrow indicates a decrease in emotional closeness.

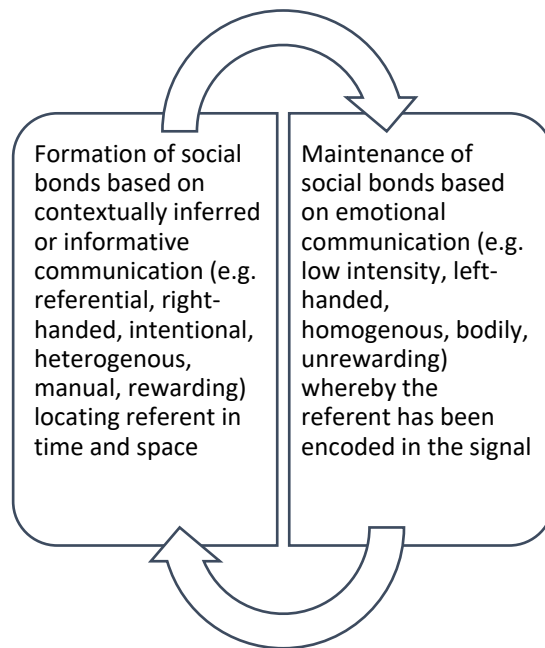


Fig. 2. Relationship between cognitive demands involved in the formation of social bonds through communication and social complexity. Top arrow indicates an increase in social complexity; bottom arrow indicates a decrease in social complexity.

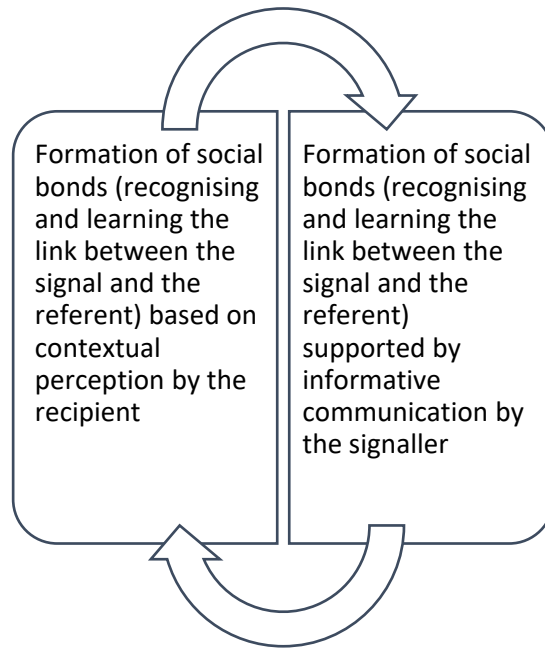
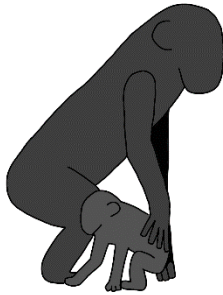
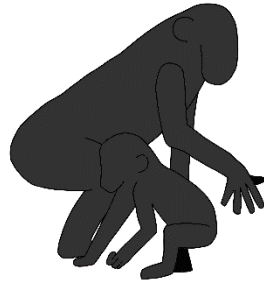


Fig. 3. Social bond formation and learning exemplified through the ‘backward sweep’ gesture. (A) The infant recognises a link between the shape and movement of the hand/arm and the referent (lowered back) in a tactile domain; (B) the infant recognises a link between the shape and movement of the hand/arm and referent (lowered back) in visual space; (C) the infant recognises that the shape and movement of the hand/arm executed without the presence of a lowered back refers to a lowered back. Image credit: Naomi Machemer.

A



B



C

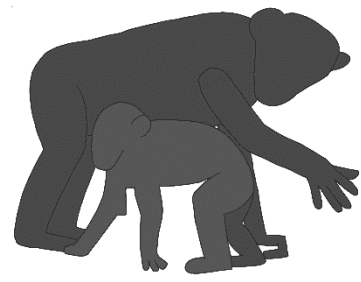


Fig. 4. Social bonding/learning positive feedback loop.

