Dominance Style and Communication in Primates

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Abstract

Dominance style (the strictness with which dominance is enforced, ranging from ‘despotic’ to ‘tolerant’) is a central feature of social relationships in many primate species, and may be an important predictor of variation in communication. However, the dominance style construct and its relationship with communication is poorly understood, particularly outside of the macaque genus. In three empirical studies, I explored the construct of dominance style and tested its relationship with communication in primates, with a special focus on chimpanzees and bonobos. In the first study, I measured dominance style and vocal communication in 111 wild groups of 26 primate species. I found evidence that more tolerant individuals vocalised at a higher rate, while more despotic species had larger repertoires of hierarchy-related vocalisations. In the second study I explored the construct of dominance style in five groups of chimpanzees and five groups of bonobos. I found evidence that, similarly to macaques, a range of behavioural measures represented a single coherent ‘dominance style’ construct in chimpanzees, while these measures represented two separate constructs in bonobos. I found no evidence that chimpanzees and bonobos differed in dominance style, but found considerable intra-species variation, particularly in chimpanzees. In the third study, I tested the relationship between dominance style and individual communicative strategies in a total of six captive groups of chimpanzees or bonobos, using a multimodal approach. I found that tolerance predicted more frequent and elaborate communication in dominant bonobos but in subordinate chimpanzees. Overall, these studies provide a comprehensive assessment of dominance style in chimpanzee and bonobos and demonstrate that dominance style is an important predictor of communication at both the individual and phylogenetic level in primates, although this relationship may vary across species.

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Author's Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

Chapter 2

The research from this chapter has been presented at a conference (European Federation of Primatology in Oxford, UK in September 2019). This chapter was a collaborative project including data contributed by collaborators across many primate field sites. I designed the research questions, requested, collated, formatted and analysed the data, wrote drafts and lead the editing process. Collaborators provided the following contributions:
Katie Slocombe: Design of research questions, intellectual advice and supervision, editing manuscript. Adriano Lameira: Design of research questions, and feedback on manuscript draft. Sally Street: advice on statistical analysis and feedback on manuscript draft. Kirsty Graham: Data coding (extracted vocal rate data from crested macaque videos) and feedback on manuscript draft. Sophie Marshall: Literature search on vocal repertoires. Susan Alberts, Elizabeth Archie and Jake Gordon: data provision on yellow baboons. All other collaborators (listed below): data provision and feedback on manuscript draft
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Chapter 3

This chapter was also a collaborative project, including data collected myself as well as data contributed by collaborators. I designed the research questions, collected data from Leipzig

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Chapter 4

I designed the research questions, collected data, created the coding scheme, coded and analysed data, wrote drafts and lead the editing process. Katie Slocombe provided intellectual advice throughout the study. Matt Henderson contributed to data collection in Vallée des Singes. Sophie Marshall and Kirsty Graham established the reliability of the coding.

Chapter 1: General Introduction

Primate Sociality

Primates are noted for being highly social at all life stages, and there exists impressive variation in their social behaviour across the order. Some species are solitary whereas others live in pairs or family units, or in groups of varying sizes comprising related and unrelated individuals (Rowe, 1996). Some group-living species exhibit fission-fusion dynamics while others remain relatively cohesive (Aureli et al., 2008). Mating systems also vary, from pair-bonded, to harem, to promiscuity (Rowe, 1996). While some species exhibit dominance hierarchies, others appear to be egalitarian (Bernstein, 1981). Other sources of variation in social relationships include the strictness of dominance relationships, relationship quality and alliance strength (Cords, 1997; Koski et al., 2007; de Waal, 1989). Considering this rich variety in the social lives of primates, it is unsurprising that there is such heavy focus on primate sociality in the literature, and how it predicts other variables such as brain size, communication and cooperation. For instance, the social brain, or the social intelligence hypothesis asserts that it is the demands of navigating a complex social world that drive the evolution of brain size and intelligence, as opposed to the need to solve ecological or foraging problems in the natural world (Dunbar, 1998; Humphrey, 1976; Whiten & Byrne, 1997). Similarly, Freeberg et al., (2012) proposed that social complexity acts as a selection pressure on communicative complexity. Evidence has been found in support of these hypotheses, but empirical research has relied heavily on using group size as the primary social measure (e.g., McComb & Semple, 2005; Barton, 1996). Group size is a useful measure in that it tells us the number of social relationships an individual has to navigate, but it does not account for the multitude of other dimensions in which sociality varies in primates. In order to gain a comprehensive and holistic understanding of species' social worlds and to understand the social context in which variables such as communication evolved, it is necessary to look further than the number of social relationships and to examine what these relationships are like.

What is dominance style?

A central feature of primate social life, and a crucial consideration when examining sociality, is that of dominance relations between individuals. Conflict and competition for resources represent unavoidable challenges in group life due to proximity of individuals. However, this proximity is thought to confer a considerable advantage on constituent members in the form of decreased predation risk (Hamilton, 1971; Treves, 1999; van Schaik, 1983), and opportunity to learn survival skills from others. The formation of dominance hierarchies allows for this proximity by providing a non-dispersive method of conflict resolution, as the hierarchy guides social interactions and allocation of resources (Preuschoft & Schaik, 2000). These conventions are beneficial to both subordinate and dominant individuals. They prevent the need for excessive aggression escalation at each conflict, which uses energy and may result in injury or fatality (Preuschoft & Schaik, 2000). Dominant individuals gain preferential access to resources, and subordinates gain some degree of tolerance from dominants by acknowledging their superior status. In this way, hierarchy adherence is an evolutionarily stable strategy. These dominance hierarchies can add layers of complexity to the social worlds of primates. Individuals must recognise their own and others' relative dominance status and behave accordingly, and may be motivated to increase their rank and engage in strategies such as coalition-formation (de Waal, 1989; Whiten & Byrne, 1997).

The degree to which hierarchies are actually enforced adds an additional layer of complexity to primate social life. De Waal (1989) noted that while dominance hierarchies are evident in all social primates, we often see a great deal of ambivalence and a much looser adherence to these hierarchies in their behaviour than might be expected. He argued that a dominant individual may sometimes be reluctant to assert their dominance with a subordinate so much that it risks compromising their relationship, as partner value plays a large role in long-term group-living. Dominants may be reliant on subordinates for agonistic support against other group members and resource acquisition, as well as the general benefits of group cohesion mentioned above. Excessive force could result in subordinates leaving to join other less restrictive groups, failing to support the dominant's rank position or even ousting them from their position through coalitionary behaviour. Put simply, "One sometimes cannot win a fight without losing a friend" (de Waal, 1989, pp.244). For these reasons, dominance relationships may vary in the degree to which dominance is actually enforced. De Waal (1989; de Waal & Luttrell, 1989) introduced the term 'dominance style' to refer to the nature of dominant-subordinate relationships in terms of how expressed behaviour corresponds with the direction of dominance asymmetry. Use of associated terminology has been inconsistent in the literature (Flack & de Waal, 2004), so I will use the terms 'despotic' and 'tolerant' to refer to relationships in which behaviour adheres to hierarchical expectations to a greater or lesser degree, respectively.

Measuring Dominance Style Across Species

Since de Waal’s earlier papers, description and measurement of dominance relationships have become increasingly precise (Flack & de Waal, 2004). Thierry's (2000) account of the social traits in macaques that covary with each other provided quantifiable measures of dominance style, allowing for testing of hypotheses relating to its causes and consequences. He identified a pattern of behavioural traits that co-vary in four clusters of what he termed ‘social styles’ (but which may now be considered synonymous with dominance styles; Flack & de Waal, 2004; Thierry et al., 2008; Zhang & Watanabe, 2014). Macaque species that are categorised into grade 1 (despotic) tend to display a strong kin bias, more unidirectional and intense but less frequent aggression, and less counteraggression, reconciliation, maternal permissiveness and tolerance around resources than those in other grades. Those in grade 4 (tolerant) display the opposite trend, and grades 2 and 3 show an intermediate pattern leaning towards the more despotic or tolerant, respectively. These behavioural traits can be used as measures of dominance style in macaques, and can be used to test the relationship between dominance style and phenomena such as communication or intelligence.

The majority of empirical work on dominance style has focused on macaque species, but there are a number of limitations in this literature that constrain our understanding of the measurement and characterisation of dominance style in these species. Firstly, dominance style of a species has largely been characterised based on social relationships between females only (Thierry et al., 2008). This may be due to historical links between dominance style literature and socioecological theories, which prioritise female social systems due to their hypothesised link with ecological variables (e.g., van Schaik, 1989). However, not only are many researchers abandoning these theories due to their increasing complexity and lack of empirical support for their predictions, but importantly, a group or species’ social environment is not limited to female-female relationships; it also includes female-male and male-male relationships. Characterising a species based on one sex provides an incomplete picture; dominance style needs to be assessed across all relationship types to gain a comprehensive description of a group or species’ social environment. Secondly, there is currently a lack of empirical examination of intra-species variation in dominance style. It is not possible to characterise a species based on a single group as studies suggest that different groups of the same species can exhibit varying dominance styles (Zhang & Watanabe, 2014). It is therefore valuable to measure dominance style across multiple groups of the same species. Finally, the co-variation of dominance style variables in macaques may not be as clear as previously thought, which may raise questions as to which behaviours best measure dominance style even in macaque species. . For instance, Balasubramaniam et al., (2012b) found that co-variation may be clearer at the extreme ends of the scale in nine macaque species. They found that counteraggression was very low in grade 1 species and very high in grade 4 species as expected, but that those in grades 2 and 3 were similar to those in grade 1, It could be that different behaviours may be more appropriate measures of dominance style for different species (e.g., counteraggression may be a good measure for Japanese but not Assamese macaques). Behaviours that co-vary with each other within a species likely form part of the same underlying construct (in this case, dominance style), and can be used to measure the construct in that species. So a valuable approach to identify the most appropriate measures of dominance style in each species would be to examine co-variation of behavioural measures among individuals within a single species.

Despite its limitations, the macaque dominance style framework provides a useful starting point for understanding dominance style across the primate order, but its application needs to be tested in other genera. Thierry (2000) explicitly stated that any extension of the dominance style framework outside of the macaque genus should be approached with caution. It is not clear whether his behavioural measures co-vary in non-macaque species, as thus far, it has only been measured in guerezas (Grunau & Kuester, 2001) and white-faced capuchins (Bergstrom & Fedigan, 2013) who were rated as extremely egalitarian, and intermediate, respectively. Bergstrom & Fedigan, (2013) suggested that Thierry's (2000) four grades may not be applicable to their capuchins as they showed some indicators of more despotic style (low counteraggression and unidirectional aggression) but others of relaxed style (low intensity aggression, low kin bias). It may be that a few, but not all, of Thierry’s traits are linked across multiple primate genera, or it may be that there are a number of smaller behavioural suites that are linked. It may be the case that there is a wider range of ways in which the hierarchy is managed. In the case of the abovementioned capuchins, it may be that subordinates have high partner value (thus explaining low kin bias), but have a low-reactivity temperament that results in high obedience to dominants (hence low counteraggression and unidirectional aggression). High intensity aggression would not be required due to high obedience, and low reactivity of dominants. In this scenario it might be expected that they would also have high reconciliation rates, as partner value is high, though this was not measured. As such they might be described as a ‘peacefully and easily enforced’ hierarchy. The picture may be more complex than four categorical grades, and factors such as partner value and reactivity may be important. To explore this issue, it is necessary to empirically examine whether Thierry’s traits do co-vary in species other than macaques. This would help to validate these measures, which would allow for the assessment of dominance style in a species and to test its relationship with variables such as communication.

Dominance Style and Communication

There is good reason to predict that dominance style is related to communication. Specifically, individuals within tolerant relationships should communicate more frequently and elaborately as tolerance is expected to both increase the pressure to communicate and alleviate constraints on communication. Within tolerant relationships, individuals are less likely to be able to achieve goals through threat of force or higher status, so there should be increased pressure to use communication to make requests. Similarly, there is likely to be a greater need to affiliate and to engage in social interactions within tolerant relationships, as this is likely to play a role alongside aggression in gaining access to food and mating opportunities, and maintaining rank (Carne, Wiper & Semple, 2011; Foste et al., 2009; Patzelt, Pirow & Fischer, 2009). Despotism on the other hand is likely to put greater constraints on communication, as individuals may be more reluctant to communicate, particularly in more elaborate ways as misunderstandings are riskier. Communication that is misunderstood or perceived as a transgression of the hierarchy by dominant partners may be more likely to be punished with physical aggression in despotic relationships. As such, tolerance should be associated with more frequent and elaborate communication.

Freeberg et al.’s (2012) hypothesis would also support greater tolerance being associated with more complex communication, due to the greater social complexity associated with tolerant relationships. While despotic relationships do involve complex social processes (e.g., rank-climbing efforts, coalitionary behaviour, social manipulation or ‘Machiavellian Intelligence’; Whiten & Byrne, 1997) tolerant relationships may be even more complex. Tolerant relationships still maintain the complexity associated with inherent dominance asymmetry and subordinate individuals must still anticipate the dominants’ behaviour and wishes (though with a less intense fear of reprimand). However, despotism by definition results in more predictable outcomes in interactions due to strict adherence to the hierarchy. So, interactions within tolerance relationships are likely to require more complex information processing due to greater social uncertainty (Barrett, Henzi & Lusseau, 2012; Ramos-Fernandex et al., 2018). There is more room to test boundaries within tolerant relationships and to vary interactions depending on motivational state and situation (e.g., hunger in the presence of food). This results in a more dynamic, changeable relationship that is ultimately more complex. To this point, Freeberg et al., (2012) argued that a greater diversity of relationships is permitted in tolerant societies as hierarchical constraints are loosened, making such societies more complex. Additionally, dominant individuals may need to consider and anticipate the behaviour and wishes of subordinates to a greater extent within tolerant relationships. In general, more social bonding is expected to occur in tolerant groups, as a wider range of close relationships are facilitated and are not restricted to close kin. For these reasons, tolerance can be used as a measure of social complexity, and should therefore predict more complex communication according to Freeberg et al.'s (2012) hypothesis.

Previous research presents a mixed account of how dominance style relates to communication in primates. Some findings in macaques suggest a link between dominance style and evolved communication systems. Dobson (2012) found that tolerance predicted a larger facial repertoire size in a phylogenetically controlled analysis of eleven macaque species. Similarly, Maestripieri (1999; 2005) found that of three macaque species, the most despotic had a smaller repertoire of gestures, while the most tolerant had the richest repertoire of assertive and submissive gestures. These studies support the hypothesis that tolerance is related to larger communicative repertoires, however some studies find that despotism is predictive of evolved communication systems. Preuschoft & van Schaik (2000) found that despotic macaque species were more likely to have formal signals of dominance status in their facial repertoires. Bouchet, Blois-Heulin & Lemasson (2013) examined three cercopithecine species in captivity and found that mangabeys had the largest and most complex vocal repertoires and they were described as the most despotic of the three species. Finally, research in baboon species suggests that dominance style may not relate to repertoire size at all. While olive, chacma and guinea baboons have different dominance styles, their vocal repertoires are largely conserved (Hammerschmidt & Fischer, 2019; Maciej et al., 2013).

The mixed evidence for tolerance being associated with larger communicative repertoires is also mirrored in the link between dominance style and communication usage, on an individual level. Of the three macaque species in Maestripieri's (2005) study, the most despotic gestured the least frequently, supporting the hypothesis that tolerance is linked to more frequent communication. However, in Bouchet et al.'s (2013) study, the more despotic mangabeys vocalised more frequently than the other two species, contradicting this hypothesis, and they also had more structurally variable threat calls. Other studies demonstrate different ways in which dominance style may be linked to communication usage. De Marco et al., (2019) found that in the despotic rhesus macaques, the strength of dominance asymmetry predicted vocal similarity between partners, but not in the more tolerant Tonkean macaques. Faraut et al., (2019) and Silk et al., (2016, 2018) found that in the more despotic chacma and olive baboons, grunts (potentially signals of benign intent) were more likely to be directed from high- to low-ranking females, while there was no effect of rank on grunt direction in the more tolerant guinea baboons. Guinea baboons also showed a lower usage of contest and display vocalisations, but more vocal signals during affiliative and greeting interactions compared to chacma and olive baboons (Maciej et al., 2013).

Overall, from this literature it is difficult to assess how dominance style relates to communication across the primate order. Most studies used small samples of closely related species, and typically did not explicitly measure dominance style, directly test its association with communication measures, or control for confounding variables such as group size or social organisation. For instance, in Bouchet et al.’s (2013) study, the mangabeys that they described as more despotic also had more complex social structure (large multi-male multi-female groups, compared the relatively smaller harem or family groups of the other two species) which could explain their more frequent and complex vocal communication. Dominance style was not explicitly measured, rather the mangabeys were simply described as having “relatively frequent peaceful and agonistic interactions and a strong hierarchy” (p. 3), which may not even fit with the definition of despotism used in other studies. To more rigorously test the relationship between dominance style and communication, it is necessary to quantify dominance style in multiple species across the primate order, controlling for other social variables such as group size.

Primate Communication

As the previous section illustrates, communication in primates is expressed though different modalities, and i research has generally focused on vocalisations, gestures and facial expressions. Broadly, communication can be defined as any signal that transmits information from sender to receiver (Marler, 1961), which can include both static signals that cannot be “turned off”, such as feather colouration, and dynamic signals which must be initiated and terminated by the signaller (Smith & Evans, 2013, p. 1390). Signals in the vocal, gestural and facial modalities fall into the latter category. The term ‘modality’ has been used with some variation in the literature, with some using it to refer to the sensory channel through which a signal is sent (Partan & Marler, 1999), and others use to describe the type of communicative act typically described in the literature in a given species (Waller et al., 2013; e.g., gestures, vocalisations and facial expressions in chimpanzees). Here I adopt the latter use, as different cognitive processes or mechanisms may underlie different communicative acts, even if emitted through the same sensory channel (e.g., gestures and facial expressions; Waller et al., 2013). Previous research has successfully revealed a wide range of abilities by studying a single modality at a time (e.g., flexibility in gestures; Hobaiter & Byrne, 2014; functional reference in vocalisations; Slocombe & Zuberbuhler, 2005; use of facial expressions to strategically influence others; Hopkins, Taglialatela & Leavens, 2011). Studies such as these using a unimodal approach represent valuable first steps in understanding primate communication and related selection pressures. However there has been a recent surge of interest in the importance of using a multimodal approach in primate research (Liebel et al., 2013 Frohlich & van Schaik, 2018; Slocombe, Waller & Liebel, 2011) which involves using the same methods to study communication from different modalities at the same time.

In order to capture the full extent of communication strategies or systems, a multimodal approach is essential. In a systematic review, Slocombe et al., (2011) found that the vast majority (95%) of primate communication studies focused on just one communicative modality, and argued that this presents some limitations. They highlighted that different methods tend to be used for studying different modalities. This creates a bias in the literature, skewing our understanding of what capacities underlie gestures, vocalisations and facial expressions. For instance, vocalisations were historically studied in urgent contexts (e.g., predator defence) which require unambiguous signalling, while gestures have been studied in relaxed contexts (e.g., play) which permit greater flexibility in signalling (Tomasello & Zuberbühler 2002). Slocombe et al., (2011) suggested these methodological differences may have contributed to conclusions that gestures can be used more flexibly than vocalisations. They also suggested that studying just one communicative modality at a time risks missing the complexity associated with the combination of signals from different modalities in a communicative interaction. Multimodal signal-use is a prime example of the type of elaborate communication that is neglected by unimodal approaches.

The term multimodal signal is defined in a number of ways in the literature. While some animal researchers define multimodal signal based on the sensory channels used in the component signals (e.g., Higham & Hebets, 2013), in primate research it generally refers to the combination of signals vocal, gestural or facial modalities (Liebel et al., 2013). Multimodal signals can be categorised as either ‘fixed’, whereby the component signals are necessary for production of the multimodal signal (e.g., a ‘pant-hoot face’ combined with a ‘pant-hoot vocalisation’), or ‘free’, whereby the component signals can be flexibly combined or produced separately (Smith, 1977). There is also variation in the operational definition of multimodal signals across studies, with some requiring the component signals to be produced simultaneously (e.g., Wilke et al., 2017) and others allowing gaps of up to 10 seconds between the components (e.g., Pollick & de Waal, 2007). In line with Wilke et al

(2017), in this thesis I focus on free multimodal signals, defining them as the combination of signals from vocal, gestural or facial modality with some temporal overlap.

Across the animal kingdom, multimodal signals may perform a range of different functions. Partan & Marler (1999; 2005) provide a framework to determine their function based on recipient responses to the multimodal signal and its unimodal component parts in isolation. They suggest that multimodal signal function can be categorised as 1) redundant, whereby the receiver produces similar responses to the multimodal signal as to the unimodal components, or 2) non-redundant, whereby the receiver produces a different response to the combined signal compared to the component signals. Figure 1 from Partan & Marler (1999) indicates these categories and sub-categories of multimodal signals. This shows that the combination of signals from different modalities offers the opportunity to produce more elaborate communication that transmits additional information, which could be useful for testing Freeberg et al.'s (2012) hypothesis.

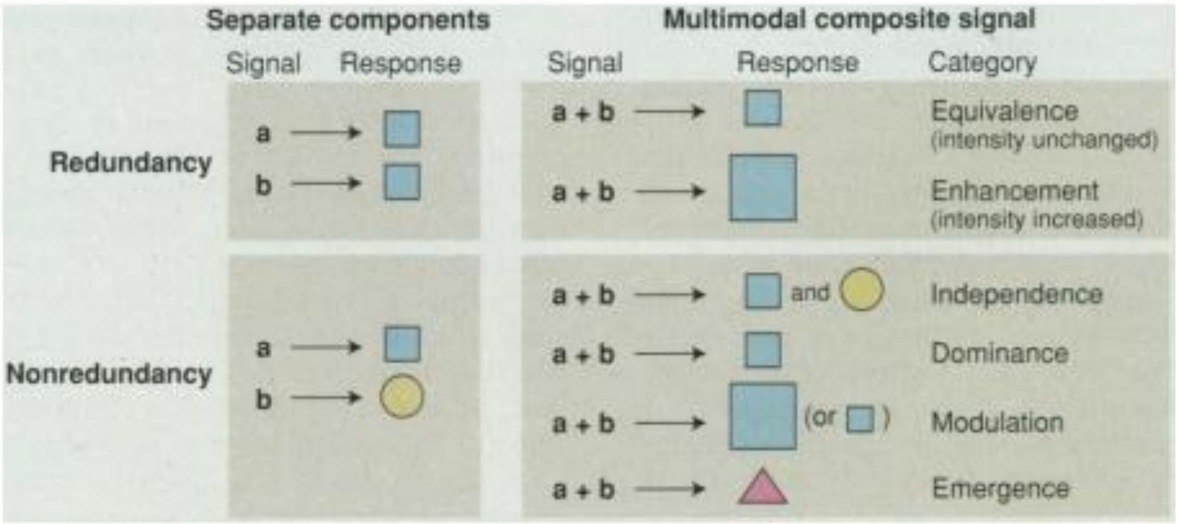


Figure 1 – Classification of multimodal signals. Figure from Partan & Marler, (1999). The same geometric shape indicates the same qualitative response; different shapes indicate different responses.

The definition and measurement of communicative complexity pose considerable challenges to tests of Freeberg et al.'s (2012) social complexity hypothesis. There is much debate as to what features of communication indicate greater complexity, but generally, communication containing a greater number of components which transmit a greater amount of information can be considered more complex (Freeberg et al., 2012; Peckre et al., 2019). Repertoire size is a commonly used measure of communicative complexity in primate species, with communication systems comprising a greater number of signal types considered more complex than smaller repertoires. Previous research does suggest that repertoire size may be a meaningful indicator of communicative complexity in primates, as they have been found to predict variables such as sociality and neural correlates in the expected direction (Dunn & Smaers, McComb & Semple, 2005). The measurement of repertoires is not always straightforward, however. Vocally graded signals are hard to categorise and most species don't have an objective repertoire based on acoustic measurements and statistical clustering techniques (Hammerschmidt & Fischer, 1998). Gestures are difficult to define, and there is no systematic agreed way of measuring them, so some repertoires are more finely split than others and most species do not have a described gestural repertoire (Cartmill & Byrne, 2011). A highly objective method for measuring facial expressions (facial action coding system; FACS; Ekman, 1997) has been developed, but this is only available for a small number of species (e.g., chimpanzees; Parr et al., 2007, rhesus macaques; Parr et al., 2010). These limitations pose challenges to the measurement of complexity in innate communicative repertoires.

Even within objectively described repertoires, the function of individual signals is often unknown and we cannot be certain that they transmit additional information. Freeberg et al., (2012) emphasised the importance of going beyond description of variation within animal signalling to quantify its complexity, and to empirically examine how signals are used and affect receiver behaviour, In order to 'decode' these signals, it is necessary to conduct careful playback experiments, or to use behavioural observations to examine receiver behaviour to a substantial sample size of signalling events. For instance, by examining recipient responses to a large sample of signalling events in wild chimpanzees, Hobaiter & Byrne (2014) identified an imperative function (e.g., 'groom me') to many gesture types. However, the function of many primate signals is currently unknown. The same issue arises with other potential complexity measures, such as the combination of signals into sequences or multimodal signals. Partan and Marler's (2005) framework to classify the function of multimodal signals has rarely been applied to primate communication, possibly due to methodological constraints (Wilke et al, 2017). As such we don't know whether combinations of signals serve different functions to their component parts. For this reason I use the term 'elaborate' to describe the diversity and combination of signal types, while remaining neutral as to whether this increases the amount of information transmitted and can thus be considered more complex. I assume that more elaborate communication has the potential to be considered more complex, but a concerted research effort assessing the amount of information transmitted in primate signalling behaviour is necessary to confirm this.

The heavy focus on the complexity of primate communication in the literature can likely be attributed to widespread interest in understanding human language evolution. As the closest living relatives to humans, comparative researchers often study primate communication to inform theories of language evolution using two primary approaches (Fedurek & Slocombe, 2011). The first approach involves studying the 'building blocks' of language in primate communication. By identifying the cognitive and communicative abilities that are shared by humans and other primates, we can estimate the abilities that existed in the last common ancestor with these closely related species. Researchers have identified key features of human language in the vocal, gestural or facial communication of primates, such as intentionality (Byrne et al., 2017; Schel et al., 2013) functional reference (Slocombe & Zuberbuhler, 2005) and linguistic laws (eg., Gustison et al., 2016; Heesen et al., 2019; Semple et al., 2010). Such research indicates that language evolution built upon these abilities after humans diverged from the rest of the primate lineage. The second approach involves identifying selection pressures that shape primate communication, and therefore potentially also human language. In this way, empirical tests of the relationship between dominance style and communication are informative for understanding human language. Testing this in species that are closely related to humans is particularly valuable. This is because with smaller phylogenetic distance there is a lower likelihood of unmeasured variables affecting this relationship.

Chimpanzees and Bonobos

As the closest living relatives to humans, chimpanzees (*Pan troglodytes)* and bonobos (*Pan paniscus)* are the ideal study subjects for scholars interested in human language evolution as they are the best models of what our last common ancestor may have been capable. Humans and *Pan* species split from a common ancestor approximately 7-8 million years ago, although estimates vary considerably (Langergraber et al., 2012). Chimpanzees and bonobos share a common ancestor with each other approximately 1.45-2.55 million years ago (Langergraber et al., 2012). Chimpanzees can further be divided into four sub-species (*ellioti, schweinfurthii, troglodytes, verus)* with a wild population totalling approximately 347,000-470,000 across 21 African countries (Humle et al., 2016). Bonobos in contrast are restricted to the Democratic Republic of Congo, with a minimum estimate of 15,000-20,000 individuals (Fruth et al., 2016). A wide literature on chimpanzee social behaviour has been developed since the 1960s, but data on bonobos is much more scarce, with only three field sites with fully habituated individuals existing today (Gruber & Clay, 2016; Stanford, 1998). Nonetheless a concerted research effort has allowed for considerable progress in comparing the two species.

Chimpanzees and bonobos share a number of similarities, including a fission-fusion society with females as the emigrating sex (Goodall, 1986; Kano, 1992), but they also share a number of important differences. In both the wild and in captivity, adult male chimpanzees form close associations with each other with a strong linear hierarchy and are dominant over all adult females (Muller, Kahlenberg & Wrangham, 2009). Females in the wild typically spend a lot of time alone or in small groups of close kin, and do not tend to form close relationships with other unrelated females, although they do appear to be more social in captivity (Parish, de Waal & Haig, 2000). In contrast, female bonobos form tight associations in both the wild and captivity, and have markedly high social status, with older females and mothers tending to be higher ranking. Although there is not complete female dominance, the most dominant individual tends to be the alpha female, with her eldest son (if she has any) often ranking behind her as alpha male (Stevens, Vervaecke, De Vries, & Van Elsacker, 2007). The lower status of male bonobos relative to their chimpanzee counterparts appears to be related to weaker social bonds; while they do frequently associate with each other and engage in affiliative behaviours, they do not support one another agonistically (Fruth & Hohmann, 2003; Ihobe & Furuichi, 1994). Their attempts at aggressive behaviour or sexual coercion appears to often be curtailed by female coalitions (Tokuyama & Furuichi, 2017). Females typically have priority of access to food, and Stanford (1998) suggested that apparent female dominance could better be explained by male deference in the feeding context. However Parish et al., (2000) argued that not only is feeding priority a fundamental feature of dominance, but males also habitually submit to dominant females outside of the feeding context. Unlike female chimpanzees, female bonobos appear to have clear control of their reproductive and social interactions (Parish et al., 2000).

Generally speaking, bonobos have a reputation as being the “peaceful ape” in comparison to chimpanzees (Furuichi, 2011; Stanford, 1998). Indeed, bonobos on average display less frequent and less intense aggression, and frequently settle conflicts through sociosexual behaviour (Furuichi, 1997; Furuichi, 2011). Unlike chimpanzees, incidence of infanticide is rare or absent, and there has been no record of intergroup killings (Fowler & Hohmann, 2010; Furuichi, 2011; Wrangham, 1999). While intergroup encounters may be tense among bonobos, they frequently result in affiliation, sociosexual interactions or even feeding together (Furuichi, 2011). It is commonly acknowledged however that lack of evidence of infanticide or intergroup killings may be a result of a lack of data in bonobos rather than lack of occurrence (de Waal, 1989; Gruber & Clay, 2016; Stanford, 1998). Stanford (1998) points out that it took more than 15 years of research including many intergroup encounters before killings were observed in chimpanzees, and wild bonobos have not been the focus of such intensive research efforts to date. Gruber & Clay, (2016) also recently argued that differences between sub-species of chimpanzees have been underappreciated, with literature being heavily biased on eastern chimpanzees. They pointed to research finding that some chimpanzees are more closely related to bonobos than other chimpanzees (Fischer et al., 2011), and particularly emphasised the contrasting behaviour of western chimpanzees whose males rarely display sexual coercion and whose females are highly sociable (Boesch, 2009; Wittig & Boesch, 2003).

Dominance Style and Communication in Chimpanzees and Bonobos

The literature on dominance style in chimpanzees and bonobos currently provides a mixed account of how dominance style can be best characterised in these species. Possibly as a result of the less aggressive impression given by bonobos, they have traditionally been viewed as having a strongly tolerant dominance style (Parish, 1996). However recent literature challenges this common view, with some suggesting that bonobos may best be described as ‘semidespotic’ (Boehm, 1999; Stevens et al., 2007). Evidence in some cases has even indicated that chimpanzees may be more tolerant than bonobos (eg., Cronin, De Groot, & Stevens, 2015; Jaeggi, Stevens, & Van Schaik, 2010). This literature must be approached with caution however for a number of reasons. Firstly, with the exception of an unpublished thesis assessing dominance style in one captive group of bonobos (Fortunato, 2009), studies have typically focused on just one or two of the dominance style traits proposed by Thierry (2000). Multiple traits are needed to gain a fuller picture of their relationships and social systems, and to examine whether Thierry’s traits do covary in this genus in the same way as macaques. Even when attempting to measure the same trait, different measures have yielded different results. For instance, some group tests have indicated greater feeding tolerance in chimpanzee (Cronin et al., 2015; Jaeggi et al., 2010), whereas dyadic measures have indicated the opposite (Hare, Melis, Woods, Hastings, & Wrangham, 2007). It is not clear however whether these results reflect differences in feeding tolerance in different contexts, or intergroup variation. Studies that have directly compared dominance style traits in chimpanzees and bonobos have typically investigated just one group at a time, but there may be considerable intraspecific variation. For instance Palagi, Paoli, & Tarli, (2004) compared the reconciliation rate of two groups of chimpanzees and bonobos. They found this conciliatory tendency (CCT) in bonobos to be 24.8%, significantly less than the chimpanzee group at 43.6%, which has been used to suggest that bonobos may be less reconciliatory than chimpanzees (Fortunato, 2009). However, CCT in chimpanzee groups have been found to range from 14.4% to 47.5%, (Fraser & Aureli, 2008;

Koski, et al., 2007; Koski & Sterck, 2007; Kutsukake & Castles, 2004; Palagi, Cordoni, & Tarli, 2006; Preuschoft, Wang, Aureli, & De Waal, 2002; Whiten & Arnold, 2001). In contrast, Fortunato, (2009) found a CCT of 40% in a group of bonobos. Dominance style may also vary between the wild and captivity; bonobo aggression appears to be more frequent in captivity, and females assert their social power more aggressively towards males (Parish, 1996). This illustrates the importance of comparing a number of wild and captive groups in each species. Such an assessment of the dominance style of chimpanzees and bonobos is valuable for testing its association with communicative strategies.

There is a wealth of literature examining chimpanzee and bonobo communication, which has revealed an impressive array of advanced communicative abilities. Both species primarily communicate through vocalisations, gestures and facial expressions (Graham, Furuichi & Byrne, 2017; Hobaiter & Byrne, 2011; Parr, Waller, Vick & Bard, 2007; Slocombe & Zuberbühler, 2010; de Waal, 1988), with olfaction being less studied and understood (Liebal et al., 2013). Their facial and gestural repertoires are very similar, but their vocal repertoires are acoustically very distinct and contain different call types (Graham et al., 2017; de Waal, 1988). Studies have demonstrated the wide range of ways in which they use and exploit these repertoires. For instance, they can use these signals to refer to external stimuli (termed 'functional reference'; Slocombe & Zuberbuhler, 2005). They can form sequences of signals, and while some gesture sequences appear to act as a fail-safe strategy for inefficient signallers (Hobaiter & Byrne 2011), there is evidence that they can extract meaning from vocal sequences (Clay & Zuberbuhler, 2011). They can combine signals from different modalities into multimodal signals (Wilke et al., 2017). An imperative function has been demonstrated in their gesture-use, which can be used to achieve clearly defined goals such as 'Groom Me' or 'Move Away', and they may persist with certain gesture types or use multiple types until they achieve their goal (Hobaiter & Byrne, 2014; Graham, Furuichi & Byrne, 2017). Such goal-directed communication combined with markers of voluntary control and social use indicate that chimpanzees and bonobos are capable of producing some signals with first order intentionality, (Demuru, Ferrari & Palagi, 2015; Leavens et al., 2005, Liebel et al., 2011; Pollick & de Waal, 2007; Schel et al., 2013). As intentionality is such a key aspect of human language production, *Pan* communication is often studied with the goal of understanding how human language evolved (Fedurek & Slocombe, 2011; Slocombe, Waller & Liebel, 2011). Despite the heavy research focus on chimpanzee and bonobo communication, and the relevance it has on understanding human language, there has been little focus on what aspects of the social environment might relate to these abilities.

Summary of Study Aims

The overall aim of this thesis was to examine dominance style and how it relates to communication in primates, with a special focus on chimpanzees and bonobos. This was addressed in three empirical studies in chapters 2-4.

The aim of chapter 2 was to test the relationship between dominance style and vocal communication across a wide range of primate species. This provided a novel test of Freeberg et al.'s (2012) social complexity hypothesis, using measures capturing the nature of social relationships as an index of social complexity instead of relying on the more crude measure of the number of social relationships in a group. Unlike previous tests of the relationship between dominance style and communication, I explicitly measured dominance style based on behavioural observations in a large sample of species, controlling for group size and phylogenetic relationship where possible. For many of the species in the sample, this was the first to measure their dominance style, representing a valuable first step in expanding this construct outside the macaque genus. The unimodal approach is this study made it feasible to acquire the largest dataset of its kind to date, and filled a gap in our understanding of the association between communication and the social lives of primates across the order. Through extensive collaboration with other researchers I collated data from 111 wild groups from twenty-six primate species. Specifically, I tested whether five dominance style variables predicted the rate of vocalising at the individual level, and three repertoire size measures at the species level. By examining individuals' dominance relationships with higher and lower ranking partners separately, I was able to gain insight into the potential reasons for the link between dominance style and vocal strategies.

In chapter 3, I took a closer look at the dominance style construct in our closest relatives, chimpanzees and bonobos. I aimed to provide a comprehensive assessment of dominance style in *Pan*, by examining how to best measure the construct, and to compare its variation between and within species. I examined the co-variation of a broad range of behavioural measures (previously used to measure dominance style in macaques) within chimpanzees and bonobos separately. This is currently lacking in the literature outside the macaque genus, and provides an indication of whether the macaque dominance style framework applies to non-macaque species. By examining multiple groups of each species, and including all relationship types (male-male, female-female and male-female), I was able to provide a more comprehensive assessment of dominance style than is available even for many macaque species. These analyses also allowed me to form dominance style indices in chimpanzees and bonobos, which can be used to quantify the construct and test its relationship with other variables such as communication. Using these findings, I compared dominance style between species, providing valuable contribution to debates related to which *Pan* species is more tolerant. Using the dominance style indices, I compared the construct between groups within the same species, between sexes, between wild and captivity, and between sub-species of chimpanzees. This study represents the most comprehensive assessment of dominance style outside the macaque genus to date.

In chapter 4, I examined the relationship between dominance style and communicative strategies in chimpanzees and bonobos. I used a multimodal approach to examine vocalisations, gestures and facial expressions as well as their combination into sequences and multimodal signals, which allowed me to capture more detailed aspects of individuals' communicative strategies than a unimodal approach would have permitted. Before examining how communicative strategies related to dominance style, I provided a detailed description and comparison of chimpanzee and bonobo communication using a multimodal approach which is currently lacking in the literature..I then used the behavioural indices that emerged from chapter 3 as quantifiable measures of dominance style in both species. Specifically, I tested the hypothesis that tolerance was associated with more frequent and elaborate communication strategies. By measuring the amount of goal-directed communication I was able to provide an indication of whether tolerance is linked to communication as a means of achieving goals.

Taken together, the three empirical chapters offer a thorough examination of dominance style and communication; using both unimodal and multimodal approaches, at the individual and species level, broadly across a wide range of species and in depth within two species, as well as in both captive and wild conditions.

Note: due to the highly collaborative nature of chapters 2 and 3, plural first person is used, while singular first person is used in chapter 4.

Chapter 2: Dominance style is a key predictor of vocal communication in non-human primates

Abstract

Vocal communication is a social affair but how the nature and quality of social relationships shape vocal use and evolution is poorly understood, limiting our understanding of how animal communication systems, including human language, evolved. Here, we use Bayesian analyses on observational data from 111 wild groups belonging to 26 nonhuman primate species, to test how vocal communication relates to dominance style (the strictness with which a dominance hierarchy is enforced, ranging from ‘despotic’ to ‘tolerant’). At the inter-individual level, we examined the link between vocal use and dominance style, and found that dominant individuals who were more tolerant vocalised at a higher rate than their despotic counterparts. However, the tolerance that subordinates received was not related to their vocal use. Our results indicate that tolerance within a relationship may place pressure on the dominant partner to communicate more during social interactions, but does not alleviate constraints on communication for the subordinate partner. At the inter-specific level, we found that more despotic species exhibited a larger repertoire of hierarchy-related vocalisations than their tolerant counterparts. Findings suggest primate signals are used and evolve in tandem with the nature of interactions that characterize individuals’ social relationships.

Introduction

The animal kingdom displays a rich array of vocal systems that vary extensively in form and function (Owings & Morton, 1998). The factors that shape the evolution and use of vocal communication are not only important for understanding animal communication systems, but are also relevant for human language evolution (Fitch, 2005). Understanding vocal communication in non-human primates (henceforth ‘primates’) is particularly important for informing theories of language evolution due to their close phylogenetic relationship to humans (Fedurek & Slocombe, 2011; Ghazanfar & Hauser, 1999). Ecological variables such as predation risk and habitat type have been found to relate to multiple aspects of primate vocalisations (eg., Brown, Gomez & Waser, 1995; Brown & Waser, 1988; Ey, Rahn, Hammerschmidt & Fischer, 2008; Maciej, Fischer & Hammerschmidt, 2011; Seyfarth, Cheney & Marler, 1980). However, given the importance of communication in navigating social interactions, much research has focused on the social variables that shape primate vocal communication, such as mating, group conflict, and social systems (eg., Hammerschmidt & Fischer, 2019; Kudo, 1987; Slocombe and Zuberbuhler, 2005, Wilkins, Seddon & Safran, 2013). Some studies of vocal communication in primates support Freeberg et al.'s (2012) hypothesis that social complexity drives the evolution of communicative complexity. For instance, McComb & Semple (2005) found that primate species that live in larger groups and that groom more frequently have larger vocal repertoires. This broad comparative study facilitates understanding of the evolution of vocal communication at the phylogenetic level. However, Freeberg et al (2012) indicated that social complexity should be associated with communicative complexity at both the individual and phylogenetic level.

In order to gain a clear insight into the individual and phylogenetic processes underlying the relationship between social factors and variation in vocal communication across the primate order, we need to examine social and vocal variables in a wide range of primate species at both the individual- and species-level. Whereas large-scale comparative studies tend to focus on vocal communication at the species-level (eg., Aureli & Schino, 2019; Hauser, 1993; McComb & Semple, 2005), most individual-level studies focus on one or a small number of species (eg., Gustison, le Roux, & Bergman, 2012, Lemasson et al., 2011). Measures of differences in vocal systems at the level of species can be captured through a variety of means such as vocal repertoire size (McComb & Semple, 2005). The variation in species' vocal systems makes it difficult to compare individual differences in many vocal measures across species, but the rate of vocalising is a measure that is directly comparable across species, and could indicate the motivation or importance of communicating for a given individual. In terms of social variables, dominance style is more amenable to measurement at both the individual and species level compared to group size for instance. Although it is considered a relationship-level construct (Flack & de Waal, 2004), empirical studies indicate that there is considerable inter-species variation in dominance style, and a species' dominance style can be quantified by examining behaviour between conspecifics (Thierry, 2007; Thierry et al., 2008). It is also possible to extract individual measures of dominance style from behaviour between dominant and subordinate individuals. As the dominance style of a relationship is dependent on the tendency or ability of the dominant partner to assert their dominance with the subordinate, only dominant partners can 'give' tolerance (e.g., by allowing or being unable to prevent aggression from the subordinate), while subordinate partners can only 'receive' tolerance. As such, two individual dominance style measures, 'given' and 'received' tolerance, can be extracted based on an individuals' interactions with lower- or higher-ranking partners, respectively.

These different levels of variation in dominance style across primates, or how this variation relates to communication, has not yet been fully explored.

Chapter 1 outlines several reasons why tolerance in relationships should be associated with more frequent and elaborate communication at both the individual and species level. Some of these reasons apply to the dominant partner and others to the tolerant partner. Within despotic relationships, dominant individuals may be more likely to use threat of force to achieve goals, or to be automatically allocated resources or receive services without need for communication (de Waal, 1986). In contrast, there may be more pressure on dominant individuals to communicate within tolerant relationships to make requests, or to elaborate in the face of an unresponsive partner, as their status alone is less likely to be effective in achieving goals, such as acquiring resources. Similarly, they may need to affiliate more with subordinates, as this is likely to play a role alongside aggression in gaining access to food and mating opportunities, and maintaining rank (Carne, Wiper & Semple, 2011; Foster et al., 2009; Patzelt, Pirow & Fischer, 2009). As such, tolerance should be associated with a higher rate of vocalising in dominant individuals, and drive a need for a more diverse range of vocal signals. For subordinate individuals, the cost of communicating may be reduced in tolerant compared to despotic relationships. If signals are misunderstood or perceived as a transgression of the hierarchy by dominant partners, they could be more likely to be punished with physical aggression in despotic relationships. As such, tolerance should also be associated with a higher rate of vocalising in subordinate individuals due to an alleviation of constraints. It is clear that both giving and receiving tolerance may result in greater usage of communication, but for very different reasons. It is therefore crucial that these two perspectives of dominance style are examined separately.

The current study aims to examine the relationship between dominance style and vocal communication at the inter-individual and inter-specific level across a wide range of primate species, and offers an empirical test of Freeberg et al.’s (2012) social complexity hypothesis for communicative complexity. Dominance style was measured through five behavioural measures (aggression symmetry, counteraggression, aggression intensity, groom symmetry and feeding proximity), whilst vocal behaviour was measured through vocal rate and vocal repertoire size. We test the hypothesis that dominance style is associated with the rate of vocalising in individuals, and with the size of vocal repertoires in species.

At the inter-individual level, we examine separately the tolerance given by dominants (“given tolerance”) and the tolerance received by subordinates (“received tolerance”) as there are different reasons for expecting dominant and subordinate individuals within tolerant relationships to communicate more frequently than those in despotic relationships.

Considering these two measures separately should also allow us to infer whether tolerance puts pressure on dominant individuals to communicate more, or whether a more tolerant social environment relaxes constraints on subordinate individuals' communication. We predicted that both i) given and ii) received tolerance would be associated with a higher rate of vocalising. We additionally predicted iii) that individuals who frequently fed close to others (another measure of tolerance) would have a higher vocal rate than those who feed close to others infrequently.

At the interspecific level, we predicted that dominance style would be associated with three aspects of vocal repertoires, all of which were obtained from previous literature. Repertoire size is one indication of communicative complexity (Freeberg et al., 2012; McComb & Semple, 2005), so we predicted iv) that more tolerant species (indicated by a higher dominance style index score) would have larger vocal repertoires. As tolerance may be most likely to act as a selection pressure on calls for managing close social interactions, we also predicted v) that any relationship between tolerance and larger repertoire size will be driven by a larger number of these 'social' calls (i.e., affiliative/agonistic signals; a subset of their overall repertoire). Finally, we predicted vi) that more despotic species (indicated by a lower dominance style index score) would have more vocal signals in their repertoires associated with the establishment and/or maintenance of the hierarchy (i.e., dominance/appeasement signals; a subset of their overall repertoire). Despotic species should have a greater need to manage and reinforce the hierarchy, putting greater selection pressure on signals associated with the hierarchy.

Methods

Study Sites and Subjects

Our sample included 111 groups of 26 species, including a diverse range of social/mating systems (family groups, harems and multi-male multi-female groups) with group sizes ranging from 3-72. We restricted the sample to wild primate groups that were habituated, non-provisioned and had some degree of dominance asymmetry in social relationships documented in the species. These criteria were chosen to ensure that all individual identities were known, and to avoid any potential effects of provisioning on dominance style. The sample included only individuals independent of their mothers, which we define as no longer depending on the mother for food, and no longer maintaining close proximity with the mother for the majority of the time. Table 1 indicates the species and other important details for all groups included in the sample. In order to ensure our datasets were representative, we imposed minimum inclusion criteria for all measures. This meant that any species, groups or individuals for which sufficient data were not available for a measure were excluded from any analyses including that measure. As aggression data were required for three out of our five measures, individuals and species with very low aggression rates are not well represented in our analysed samples.

Table 1

Details on species included in sample.

Family	**Species**	**N Groups**	**Group Size mean (SD)**
Hominidae	*Pan paniscus*	1	24
	Pan troglodytes schweinfurthii	2	40.50 (2.50)
	Gorilla beringei beringei	1	13
	Gorilla gorilla gorilla	1	6
Cercopithecidae	*Cercocebus atys*	1	65
	Cercopithecus ascanius	2	18.50 (6.50)
	Cercopithecus campbelli	2	7.5 (1.5)
	Cercopithecus diana	2	10.50 (0.05)
	Chlorocebus pygerythrus	2	23 (11)
	Chlorocebus pygerythrus	1	67
	Macaca assamensis	1	65
	Macaca fuscata yakui	3	26.67 (8.01)*
	Macaca nigra	2	54 (11)
	Macaca radiata	3	18 (5.72)
	Macaca sylvanus	2	24.5 (4.5)
	Papio anubis	3	26.00 (9.1)
	Papio cynocephalus	5	53.60 (10.87)
	Papio kindae	1	78
	Theropithecus gelada	38	10.24 (4.70)
Platyrrhini	*Alouatta pigra*	3	5.33 (1.25)
	Ateles geoffroyi	1	19.00 (1.00)
	Cebus imitator	3	22.67 (4.02)

Lemuroidea	*Eulemur mongoz*	2	4 (0)
	Eulemur rufifrons	4	8.75 (2.49)
	Indri indri	7	3.71 (0.70)
	Lemur catta	5	12.40 (2.87)
	Propithecus verreauxi	14	6.14 (2.10)

Ethics

This study was approved by the University of York Animal Welfare and Ethical Review Body (AWERB), and data collection for all groups was approved by the relevant authorities and ethical bodies (see appendix 1).

Dominance Style Data

Data Collection

As this study was a collaborative effort, it includes a mix of data that were obtained specifically for the current study, and data already collected for unrelated projects. For this reason not all behavioural measures were available for all groups, and there was variation in data collection methods and behavioural definitions (e.g., different inter-bout intervals). To ensure comparability of measures across individuals, groups and species, we did not extract variables that were affected by these differences (e.g. aggression rate) and excluded data that could not be made comparable (appendix 2 indicates the data available for each group/species and reasons for missing data).

Aggression.

Species-typical aggressive behaviour was recorded using focal, all-occurrence or *ad libitum* sampling methods (see appendix 3 for ethograms, and appendix 4 for observational methods used for each group). We defined an aggressive bout as all aggressive behaviour that occurred in a dyad separated by 10sec-5min depending on group (see appendix 4 for time criterion used for each group). The initiator of the bout was considered the aggressor and the initial recipient of the aggression was the victim. For each bout we recorded the identities of the aggressor and victim, whether the aggressor used physical contact, and whether the victim retaliated, fled or submitted. Bouts where the aggressor and victim could not be identified were excluded.

Grooming.

Grooming data were recorded using all-occurrence or focal methods (see appendix 4 for methods used). A grooming bout was defined as all grooming behaviour between two individuals separated by 10-60sec depending on group (all role changes and mutual grooming considered part of same bout; appendix 4 for time criterion for each group).

Proximity During Feeding.

Instantaneous point samples of the distance between a focal individual and its nearest neighbour were recorded while the focal was in a feeding context (see appendix 4 for intervals of scans across groups).

Dominance Style Measures

From the data we extracted five dominance style variables: aggression symmetry (i.e., aggression Directional Inconsistency Index; DII), counteraggression, aggression intensity, and feeding proximity are all commonly used dominance style variables (e.g., Balasubramaniam et al., 2012; Cronin, Van Leeuwen, Vreeman, & Haun, 2014; Hare, Melis, Woods, Hastings, & Wrangham, 2007; Thierry, 2000; de Waal & Luttrell, 1989) and grooming symmetry (i.e., groom DII) is a previously unused but potentially useful measure of dominance style. High-ranking primates tend to receive more grooming (Schino, 2001; Seyfarth, 1977) so greater symmetry in the direction of grooming within a dyad could indicate a more tolerant relationship. For all variables, only interactions with other independent individuals were considered. Four of these variables (aggression symmetry, counteraggression, intensity and grooming symmetry) were ultimately extracted in three forms, or 'measures'; a species level measure, and at the individual level a 'given tolerance' measure and a 'received tolerance' measure. Feeding proximity was extracted separately only as an individual level measure.

At the individual level, given and received tolerance measures were determined in the following ways: (i) To calculate given tolerance for a given individual (e.g. individual A), on grooming and aggression DII measures we took a mean value of all dyads including the individual and a lower-ranking partners (B,C,D); (ii) To calculate received tolerance for a certain individual on the same measures (e.g. individual D), we took a mean value of all dyads including the individual and higher-ranking partners (A, B, C); (iii) To calculate given tolerance for a given individual (e.g. individual A) on counteraggression, feeding proximity and aggression intensity measures we took the sum of all events involving lower-ranking partners (B,C,D) to calculate an overall proportion (e.g. A receives counteraggression in 2/10 events with B and 6/12 events with C, A's final score will be 8/22); (iv) To calculate received tolerance for a certain individual on the same measures (e.g. individual D), we took the sum of all events involving higher-ranking partners (A, B, C). To determine the dominance ranks of individuals in each group we calculated modified David's scores (De Vries, Stevens, & Vervaecke, 2006) using SOCPROG on Matlab (Whitehead, 2009) based on decided aggressive bouts (winner determined by the victim fleeing or submitting). We necessarily had to exclude individuals without the required flee/submission data (excluding 1 species).

A species level measure was extracted from four of the five dominance style variables (excluding feeding proximity as there were only eight species with data for this variable) and combined into a dominance style composite index per species. To calculate a species level measure we took the following steps. First we calculated individual scores for (i) each dyad in the group (for both DII measures) or (ii) each individual in a group (a mean of their scores from interactions with all group members). To calculate the group score we took a mean of all individual scores, or all dyads for both DII measures. To ensure group scores were representative, for a measure to be calculated for a group, we required that data were available for at least 10 individuals (if group size was 20+) or 30% of the group (if group size was smaller than 20). Lastly, to calculate the species level measure we took a mean of all the group scores for that species. In order to calculate a dominance style composite index for each species, we took the following steps: We first took all the species measures and standardised each measure (e.g. aggression symmetry) across all species to form Z-scores and reversed the aggression intensity score. We then found the mean of all standardised measures available per species to calculate their dominance style composite score, with a higher score indicating greater tolerance. A minimum of two measures was required for a species to be included in the composite measure.

Aggression Symmetry.

Aggression symmetry was measured by aggression DII, which refers to the proportion of bouts within a dyad in which the roles of aggressor and victim occurred in the least frequent direction (de Waal, 1977; Noë et al., 1980). In an example where Individual A initiated aggression with Individual B fewer times than vice versa, the aggression DII for this dyad would be calculated by the following formula:

$$\frac{\text{N bouts A aggressed B}}{\text{Total N aggressive bouts between A and B}}$$

Values could range from 0-0.5, with a higher value indicating greater relationship symmetry, and therefore greater tolerance. Only dyads with two or more bouts of aggression were given an aggression DII score.

Counter-aggression.

The counter-aggression variable refers to the percentage of aggressive bouts that an individual initiates (in the role of aggressor) in which the victim retaliates. A higher value indicates greater tolerance. We excluded bouts recorded *ad libitum* as the saliency of these behaviours could have biased the resulting values. A minimum of 2 aggression bouts per individual were required for the individual to obtain a value for this measure. An individual's 'given tolerance' score for counteraggression was the percentage of aggressive bouts that they initiated (in the role of aggressor) against a lower ranking individual, in which the victim retaliated. An individual's 'received tolerance' score for counteraggression was the percentage of aggressive bouts in which they retaliated against a higher-ranking aggressor.

Aggression Intensity.

Aggression intensity refers to the percentage of bouts that than individual initiates (in the role of aggressor) in which they used physical contact. A lower value indicates greater tolerance. We excluded bouts recorded *ad libitum* as the saliency of these behaviours could have biased the resulting values. A minimum of 2 bouts per individual was required for the individual to obtain a value for this measure. An individual's 'given tolerance' score for intensity was the percentage of aggressive bouts that they initiated (in role of aggressor) against a lower-ranking victim, in which they used physical contact. An individual's 'received tolerance' score for intensity was the percentage of bouts where they were the initial victim to a higher-ranking aggressor, in which the aggressor used physical contact.

Grooming Symmetry.

From the grooming data we measured grooming symmetry by calculating groom DII for all dyads possible, which is the proportion of grooming bouts in which the role of giver and recipient of grooming occurred in the least frequent direction. It is calculated in the same way as aggression DII, and only dyads with two or more grooming bouts were given a grooming DII score.

Feeding Proximity.

The percentage of scans in which an individual was within 1m of another independent individual whilst feeding was calculated as a measure of feeding proximity. A minimum of 10 scans was required for an individual score to be calculated for this measure. Feeding proximity was excluded from any models or calculations of given and received tolerance and was treated separately as an individual level dominance style measure potentially encompassing both given and received tolerance. This is because for many datasets we could not ascertain whether individuals other than the nearest neighbour were within 1m, so could not reliably determine the percentage of scans within 1m of a higher or lower ranking individual. Feeding proximity was not calculated at the species level as there were too few species with data for this measure to merit doing this.

Vocal Communication Data

Vocal Rate.

For each group, vocal rate data were collected during an observation period that overlapped with that of the dominance style data collection. From focal observations (see appendix 4 for length of focals in each group) we measured the number of vocal bouts produced by each individual per hour. We defined a vocal bout as all vocalisations produced by the individual within 30 seconds of one another, regardless of vocalisation type or context. We restricted our definition to rely solely on a time criterion in order to ensure consistency across primate species with varying vocal repertoires and use of sequences. A minimum of 2 hours focal observation time was required for inclusion of an individual (see appendix 2 for focal observation time in each group).

Vocal Repertoires.

We extracted data on the vocal repertoire of each species from previous literature. We acknowledge that there currently exists a certain degree of subjectivity in the description of species-typical vocal repertoires in the literature (Fischer, Wadewitz & Hammerschmidt, 2017; Gamba et al,. 2015; Peckre et al., 2019). For this reason, we followed McComb & Semple’s (2005) criteria for selection of repertoires and call types as closely as possible (see appendix 5 for publications used per species and necessary deviations from their criteria for our sample of species). This ensured the highest degree of comparability across species that is possible from the current repertoire literature. Following McComb & Semple, (2005) we only included repertoires which distinguished calls based on acoustic description for which the whole adult repertoire was described. One species (*Propithecus verreauxi*) was excluded for all repertoire analyses as it had no published repertoire. We also followed the rules outlined by McComb & Semple (2005) for inclusion of call types to calculate repertoire measures, which meant we included all calls produced by adults, excluding lip-smacking, teeth chattering/grinding and vomiting, and we considered calls consisting of multiple vocal units as separate calls if these units had not previously been described as distinct calls in the repertoire.

We extracted three vocal repertoire measures for each species; the overall repertoire size, the number of social calls and the number of hierarchy-related calls in the repertoire (the latter two measures being subsets of the overall repertoire size). We categorised calls as social or hierarchy-related based on the description of the contexts in which the calls occur in their associated repertoire paper. Calls that are described as occurring in an affiliative or agonistic context were classed as social calls, and calls described as occurring in an appeasement or dominance context were classed as hierarchy-related signals (see table 2 for definitions of these contexts). These call-types were not mutually exclusive (e.g. some calls met the definitions for inclusion in both social and hierarchy-related repertoires).

Table 2

Definitions of Social and Hierarchy-Related Signals

	Context	**Definition**
Social Calls	Affiliative	Study refers to call being associated with affiliation or with an affiliative behaviour (e.g., embrace, groom, play), with bonding, greeting or approach, or as a signal of benign intent.
	Agonistic	Study refers to call being associated with agonism, aggression, attack, fight, threat or conflict, not including inter-group interactions, or where the study specifies that the caller is not involved in the interaction (e.g., watching a fight).

Hierarchy-related calls	Appeasement	Study refers to call being associated with appeasement, with a submissive posture or with being produced by a subordinate or directed towards a dominant individual.
	Dominance	Study refers to call being associated with dominance, with dominating another individual, or with being produced by a dominant or directed towards a subordinate individual.

Data Analysis

Individual Level Analyses.

To test our individual level predictions that i) given tolerance and ii) received tolerance would predict vocal rate, we constructed two generalised linear mixed models (GLMMs) with vocal rate as the dependent variable, either the four given or the four received tolerance measures (Counteraggression, Aggression Intensity, Aggression DII and Groom DII) and group size as fixed effects, and group and species identities as random effects. We fitted these models in R in a Bayesian framework, with the package MCMCglmm (Hadfield, 2010). We also tested whether (iii) feeding proximity predicted vocal rate. As this variable could potentially encompass both given and received tolerance, it was entered into a separate GLMM as a fixed effect. See table 3 for summary of these models.

MCMCglmm provides a flexible platform for comparative analyses as it allows both for modelling non-linear relationships and incorporating random effects, including phylogenetic error structures and within-species variation (Hadfield 2010). For relatively small (~30 or fewer) samples of species, however, phylogenetic signal cannot be reliably estimated (Freckleton, Harvey, & Pagel, 2002). One potential solution to this problem would be to fix phylogenetic signal to the maximum value of 1, but this functionality is not implemented in MCMCglmm (Hadfield & Nakagawa 2010). This is possible using phylogenetic generalised least squares (PGLS) regression (Grafen 1989), but PGLS does not allow for multi-level models incorporating random effects. Currently, as far as we are aware no existing R package allows us both to incorporate random effects such as species identity as well as a phylogenetic error structure with phylogenetic signal fixed to the maximum value. Our inclusion of species as a random effect, however, controls for phylogenetic nonindependence to some extent (as in Sol and colleagues, 2012, for example). We estimated only random intercepts for group- and species-level effects as we had no *a priori* reason to expect variation in slopes for the fixed effects across groups and species and because this would result in overcomplicated and underpowered models (see table 3 for ratio of parameters to sample size in all main models).

For all models we used default diffuse normal priors for the fixed effects and commonly used inverse Wishart priors for the random effects and residual variance (setting V=1 and nu=0.002; Hadfield, 2010). All models were run for 501000 iterations, sampling every 100 generations, with a burn-in period of 1000 iterations, which was sufficient to achieve effective sample sizes of >1000 for all parameters. Variance inflation factors (VIFs) for all analyses were low (<2), indicating that multicollinearity was not an issue. To assess the appropriateness of the models for the data, we checked the distribution of the dependent variable and the model residuals, chain plots, and plots of fitted vs. observed values of the dependent variable. For many models, no distribution indicated an ideal fit to the data, but a Gaussian distribution with a log10 transformation was a reasonable fit to the distribution of the dependent variables (see appendix 6 for diagnostic plot examples). As such, we report results from models in the main text but also illustrate the robustness of any effects we find by providing results using alternative models in appendix 7. For all models, we report posterior means, 95% credible intervals and pMCMC values for the fixed effects. pMCMC values indicate the probability that the value of a parameter is zero.

Species-Level Analyses

To test whether dominance style predicts iv) the overall vocal repertoire size, v) the number of social vocalisations or vi) the number of hierarchy-related vocalisations in a species repertoire, we fitted species-level models with each of the three corresponding repertoire size measures as the response variables, and group size (mean of all groups in species) and the dominance style composite index as fixed effects. As in the individual level analyses, we were unable to accurately estimate phylogenetic signal in the species level analyses due to insufficient sample size. However, since we did not require random effects for group and species in the species-level analyses, we were able to use frequentist phylogenetic generalised least squares (PGLS) models fixing Pagel’s λ to 1, implemented in the caper R package (Orme et al., 2013, RStudio Team, 2015). This highly conservative approach assumes that phylogeny has the maximum possible influence over the species’ residual variance in the model. One species (*Papio kindae)* was excluded from PGLS analyses as it is not included in the phylogeny (Arnold, Matthews & Nunn, 2010). In line with the MCMC models, we used a log10 transformation on the outcome variable in the PGLS models. Where the dominance style composite index had a significant effect on the outcome variable (p <.05), we implemented separate PGLS models with each of the individual dominance style measures as a predictor instead of the composite index (excluding group size as a predictor in models with aggression intensity and counteraggression due to insufficient sample size). See table 3 for summary of main models.

Table 3

Summary of main individual and species level models

Main Individual Level Models (Bayesian MCMC GLMMs)

	Dependent Variable	**Random effects**	**Fixed effects**
i) Given Tolerance full model* (N=162 individuals from 14 species)	Vocal Rate	Group Species	Aggression DII Counteraggression Aggression Intensity Groom DII Group Size
ii) Received Tolerance full model* (N=147 individuals from 12 species)	Vocal Rate	Group Species	Aggression DII Counteraggression Aggression Intensity Groom DII Group Size
iii) Feeding Proximity model (N=240 individuals from 8 species)	Vocal Rate	Group Species	Feeding Proximity Group Size

Main Species Level Models (Frequentist PGLS models with Pagel's λ=1)

	Dependent Variable	**Fixed Effects**
iv) Overall Repertoire Size (N=20 species)	N calls in repertoire	Dominance Style Composite Index Group Size
v) Social Call Repertoire Size (N=20 species)	N affiliative or agonistic calls in repertoire	Dominance Style Composite Index Group Size
vi) Hierarchy-Related Call Repertoire Size (N=20 species)	N Hierarchy-Related Calls	Dominance Style Composite Index Group Size

Note: *Given tolerance form of dominance style variables used as fixed effects in the given tolerance model, and the received tolerance form in the received tolerance model.
MCMC = Monte Carlo Markov Chain
GLMM = Generalised Linear Mixed Model
PGLS = Phylogenetic Generalised Least Squares

Results

Individual-Level Analyses

Given Tolerance.

To test the prediction that dominant individuals who are more tolerant of subordinate partners vocalise more frequently than their despotic counterparts, we constructed a GLMM with group size and the four given tolerance measures as fixed effects, group and species as random effects, and vocal rate as the dependent variable (see appendix 8 for species and groups included in all models). In support of our prediction i), we found that individuals with higher given tolerance, in terms of more symmetrical aggression, vocalised more frequently (see table 4). However, no clear relationship was found between vocal rate and the other three given tolerance measures or group size. Figure 2 displays the posterior distributions for the beta coefficients for all fixed effects in this model.

As an individual had to have data for all four given tolerance measures to enter this model, 91 individuals and five species with aggression symmetry data were excluded. To check that this finding generalised to the wider number of individuals and species with these data available, we ran a further model with just aggression symmetry as the fixed effect and vocal rate as the dependent variable (with groups and species as random effects) on 253 individuals from 19 species. This model also indicated that aggression symmetry was an important predictor of vocal rate (see appendix 7), indicating that this finding is generalizable across our full sample of individuals with aggression symmetry data. Overall, our results indicate that dominant individuals whose aggression is more symmetrical with that of lower ranking partners vocalise at a higher rate.

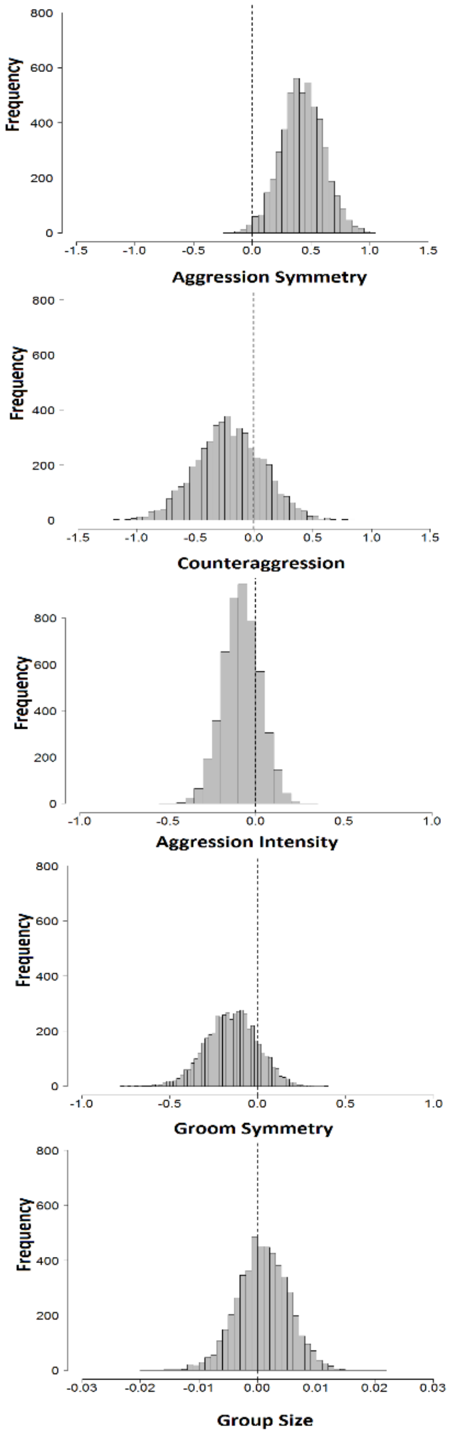


Figure 2 Posterior distributions of beta coefficients for the effects of aggression symmetry, counteraggression, aggression intensity, groom symmetry (given tolerance measures) and group size on vocal rate. The distribution for aggression symmetry is shifted substantially away from zero, indicating evidence for an effect in the corresponding direction. Distributions for the other variables are centred closer to zero, indicating little or no evidence for effects.

Table 4

Results of MCMC model with given tolerance measures as fixed effects (N individuals=162, N groups = 41, N species = 14). Random effects of group and species explained 30% and 42% of variance, respectively, while fixed effects explained 6% of variance. Note that as species and group explained a relatively large amount of variance (likely due to phylogenetic ancestry and ecological conditions), by necessity the behavioural measures must explain a relatively small amount, but this does not mean they are biologically insignificant.

	Variable	**Posterior Mean β**	**1-95% CI**	**u-95% CI**	**pMCMC**
Fixed Effects	Aggression Symmetry	0.42	.09	.79	.02
	Groom Symmetry	-.15	-.41	.15	.31
	Counter-aggression	-.22	-.75	.34	.44
	Aggression Intensity	-.09	-.28	.12	.43
	Group Size	<.001	-.01	.01	.84

Received Tolerance

To test the prediction that subordinate individuals are free to vocalise more frequently if dominant partners are more tolerant of them, we constructed a GLMM with group size and the four received tolerance measures as fixed effects, group and species as random effects, and vocal rate as the dependent variable. Contrary to our prediction v), we found no clear relationship between vocal rate and any of our received tolerance measures (see table 5). Hence, we found no strong evidence that subordinate individuals vocalised more frequently if dominant partners were more tolerant towards them.

Table 5

Results of MCMC model with received tolerance measures as fixed effects (N individuals = 147, N groups = 38, N species = 12). Random effects of group and species explained 19% and 48% of variance, respectively, while fixed effects explained 9% of variance.

	Variable	**Posterior Mean β**	**1-95% CI**	**u-95% CI**	**pMCMC**
Fixed Effects	Aggression Symmetry	.14	-.20	.48	.42
	Groom Symmetry	-.26	-.57	.07	.13
	Counter-aggression	-.05	-.67	.53	.88
	Aggression Intensity	-.02	-.22	.17	.81
	Group Size	.004	-.004	.01	.33

Feeding Proximity

To test the prediction iii) that individuals who tend to stay close to other group members during feeding also vocalise more frequently, we examined the relationship between feeding proximity and vocal rate in a GLMM with group size and feeding proximity as fixed effects, group and species as random effects and vocal rate as the dependent variable. Our model indicated that feeding proximity was not associated with vocal rate (N individuals = 232, N groups = 37, N species = 8, Posterior Mean β = -.004, pMCMC = .97), and random effects of group and species explained 5% and 75% of variance, respectively. This means that we found no support for our prediction that individuals who frequently feed close to other individuals vocalize more frequently.

Species Level Analyses

We examined whether species' dominance style was related to three vocal repertoire measures; iv) overall vocal repertoire size, v) number of social calls in the repertoire, vi) number of hierarchy-related calls in the repertoire, in the twenty species with the required data. To do this we implemented three PGLS models setting lambda to 1, with the dominance style composite index and group size as predictor variables, and each of the three vocal repertoire measures as the dependent variables. Figure 3 illustrates the spread of values of the dominance composite index across species in the primate phylogenetic tree.

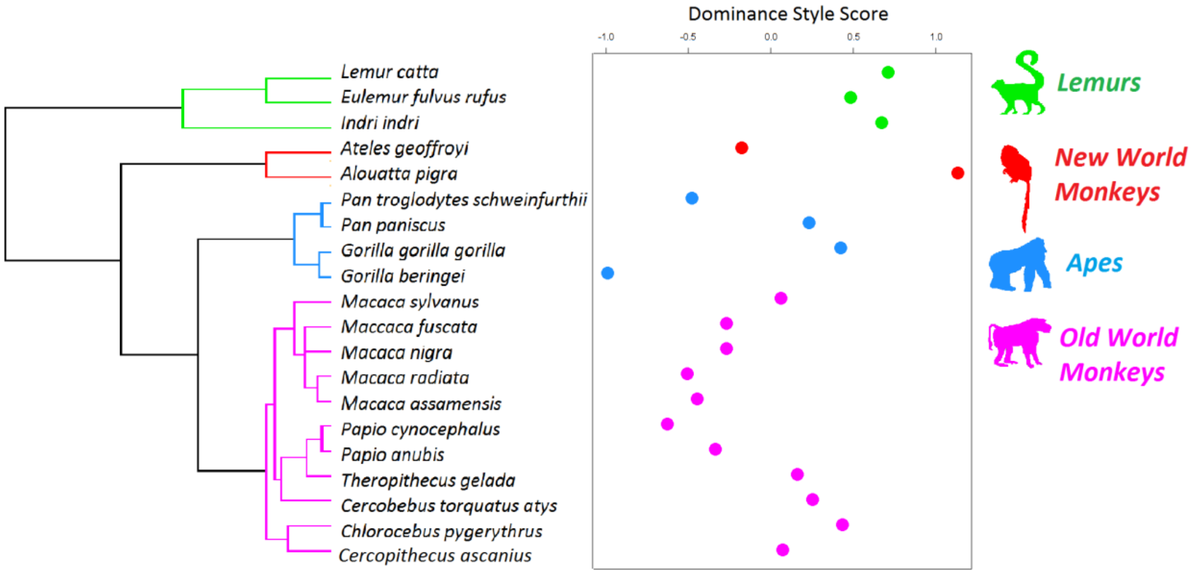


Figure 3 Dominance Style Composite Index values across species in the sample for which phylogenetic information was available. Positive index scores indicate tolerance, whilst negative index scores indicate despotism. The cladogram on the left displays the species' binomial names organised according to phylogenetic distance.

We found no support for our predictions that more tolerant species would have larger vocal repertoires or more social calls in their repertoires (overall repertoire: β=0.08, p=.400. social calls: β=0.43, p=.740), but did find support for our prediction that more despotic species had more hierarchy-related calls (β= -0.58, p=.002). Figure 4 displays the relationship between the number of hierarchy-related calls and the dominance style composite index.

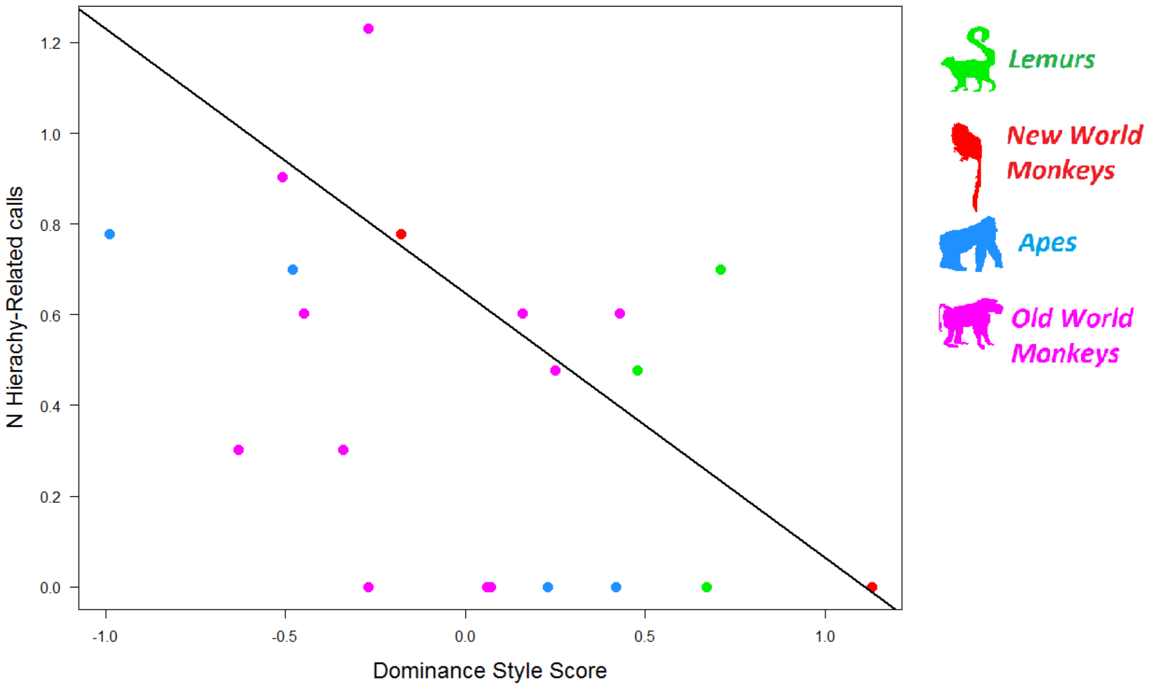


Figure 4 - The relationship between the number of hierarchy-related calls in the species repertoire with their dominance style composite index score. Positive index scores indicate tolerance, whilst negative index scores indicate despotism. Each point represents a species. In line with the PGLS models, a log10 transformation was made on the N of hierarchy-related calls. The black line of fit is from the PGLS model vi) which assumes maximum phylogenetic inheritance

To see which individual dominance style measure most strongly predicts the number of hierarchy-related signals, we constructed separate models including each of the four dominance style measures separately instead of the dominance style composite index. We found that aggression intensity, grooming symmetry, aggression symmetry and group size did not significantly predict repertoire size of hierarchy-related signals. However, low counteraggression, indicating greater despotism, was related to a larger repertoire of hierarchy-related calls (N=16 species, β = -2.35, p=.02). Overall our results indicate that more despotic species have richer repertoires of hierarchy-related calls, and counteraggression is the dominance style measure that most strongly predicts this relationship. Contrary to our expectations, however, our results provide no evidence that more tolerant species have more complex communication systems in the form of larger vocal repertoires or a larger range of social calls in their repertoires.

Discussion

The goal of this study was to examine the extent to which dominance style explains variation in the diversity and usage of vocal signals across the primate order. Using a rich behavioural dataset from twenty-six primate species, we found evidence that dominance style was related to vocal communication at the inter-individual and inter-specific level. Notably, we found that more despotic species had richer repertoires of hierarchy-related calls in their evolved vocal systems, but that individuals who were more tolerant of lower-ranking partners vocalised at a higher rate. As the level of tolerance an individual receives from higher-ranking partners did not predict their rate of vocalising, we infer that tolerant relationships are more likely to place pressure on dominant individuals to communicate than to alleviate constraints on subordinate individuals. Our findings suggest that the strictness of the dominance relationships of individuals and species provides important context for understanding primate vocal usage and evolution.

We found that individuals vocalised at a higher rate if they had more symmetrical aggression with subordinate partners (an indication of greater tolerance). This finding is consistent with the hypothesis that tolerant individuals likely have a greater need to communicate in order to manage interactions with more uncertain outcomes, to affiliate with a wider range of individuals, or to request resources and services, rather than relying on higher dominance status and/or brute force. However, we did not find support for our prediction that subordinate individuals would also vocalise more if their relationships with dominant partners were more tolerant. One could perhaps conceive that, for subordinate individuals, there would be a similar need to negotiate and affiliate regardless of the tolerance of dominant partners. Compared to dominant individuals, subordinates are likely to be under increased pressure in any social environment to take the perspective of others, a skill that requires complex social information processing (Galinsky et al., 2006). As such, receiving tolerance may not increase social complexity for individuals as strongly as giving tolerance, hence no clear effect of received tolerance on the rate of communicating. We emphasise that we did not find clear evidence against a relationship between received tolerance and vocal rate, but our findings indicate that tolerance is linked to vocal communication more strongly as a result of increased pressure than alleviation of constraints.

Our results provide evidence that despotism co-evolves with a greater diversity of hierarchy-related communicative signals. We found that more despotic species had larger repertoires of dominance and appeasement vocalisations. This result supports Preuschoft & van Schaik's (2000) finding that despotism predicted the existence of formal facial signals of dominance status in a species. However, in contrast to these formal status signals, which are by definition produced uni-directionally (Preuschoft, 1999; Preuschoft & van Schaik, 2000; de Waal & Luttrell, 1985), the hierarchy-related vocalisations we considered were not necessarily completely unidirectional. As such, it remains possible that homologous vocalisations are present across species, and despotism is related to the asymmetry in use of these vocalisations between dominant and subordinate individuals, rather than driving the evolution of the signals themselves. This 'homologous signal' argument was made by Preuschoft & van Hooff (1995) to explain the differential use of similar facial displays across species with different dominance styles; notably the 'silent bared-teeth display' which is used symmetrically and flexibly in tolerant species but asymmetrically and in narrow contexts in despotic species. To our knowledge, our study is the first to indicate that despotism is associated with a richer repertoire of hierarchy-related vocalisations, but future research should establish whether these vocalisations have homologues in more tolerant species that are produced more symmetrically within dyads.

Our species level findings did not provide support for the social complexity hypothesis (Freeberg et al., 2012). Despite more tolerant individuals vocalising at a higher rate, we did not find that more tolerant species had larger overall vocal repertoires or more social vocalisations in their repertoires. Despite our efforts to maintain the highest degree of comparability across research groups, the inevitable noise associated with variation in data collection protocols across this large collaborative dataset could be a contributing factor to our nulls results. Perhaps more importantly, however, if tolerance is not stable across generations, this may explain why tolerance concurrently predicts vocal usage, but not the complexity of the evolved vocal system. It would be necessary for tolerance to remain stable in a species long enough to act as a selection pressure on its innate communication system. However, inter-group variation within a species has been found (Zhang & Watanabe, 2014), indicating the potential for instability across generations. Future research should identify species with stable dominance style and test the relationship between tolerance and communication systems in these species. Game theory models indicate that a despotic strategy may be more stable than a tolerant strategy (Matsumura, 1999; Matsumura & Kobayashi, 1998), which could explain why we found stronger evidence for despotism being related to evolved communication systems than tolerance.

Surprisingly, we did not find that group size, a commonly used measure of social complexity, was associated with any vocal measure, including repertoire size. In fact, contrary to McComb and Semple’s (2005) findings, when we plotted the data we found a slight negative relationship between group size and repertoire size (see appendix 9). This difference between studies may be due to the samples of primates used varying in size and composition and discrepancies in estimates of repertoire size and group size. Comparing our sample with those from McComb & Semple (2005) and Dunn & Smaers (2018), group size estimates for some species are considerably different. For instance, bonobos feature in all three studies, but were reported to have group sizes of 24, 125 and 43, respectively. This highlights the importance of obtaining and using accurate group size measures, and incorporating intra-species variation in group size. Additionally, a concerted research effort is required to ensure objective vocal repertoires based on acoustic measurement and statistical classification of call types are available for each species (Gamba et al., 2015; Wadewitz et al., 2015).

We hope that our findings encourage further examination into the strictness of dominance relationships and communication across the animal kingdom. Asymmetrical dominance relations are observable not only in primates, but in a wide range of animal taxa (eg. birds; Piper, 1997; elephants; Archie et al.,2006; pigs; Meese & Ewbank, 1973). As such, how communication is related to dominance style in these species could be investigated. Our focus on nonhuman primates also begs the question of how dominance style may relate to human language and communication. Humans are thought to have lived in highly tolerant societies in our recent evolutionary past (Boehm, 1999), so how dominance style might have contributed to the evolution of human language is an exciting prospect for further examination.

Taken together, our findings indicate that dominance style is an important social variable to consider for understanding vocal usage and evolution in nonhuman primates. While greater tolerance predicts individual variation in vocal rate, greater despotism predicts a key aspect of the evolved vocal system (i.e., larger diversity of hierarchy-related vocal signals). Our findings that given but not received tolerance predicts vocal rate hints that the proximate cause of the relationship between tolerance and vocal usage is more strongly related to an increased pressure to communicate rather than alleviation of social constraints across primate species. This study is the first to assess the relationship between dominance style and communication across multiple primate genera with a multiple-levels-of-analysis approach, providing valuable insights into the pressures shaping primate vocal communication. This is essential for examining other potential correlates of dominance style, such as brain size or ecological factors, or to further explore its relationship with communication by using a multimodal approach (Liebal et al., 2014; Peckre et al. 2019, Slocombe et al., 2011). If we are to understand the effects of social complexity on the evolution of communication, we need to move beyond a narrow focus on group size, and incorporate measures of the nature of social interactions, such as dominance style.

Chapter 3: An assessment and comparison of dominance style in chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*)

Abstract

Dominance style (the strictness with which dominance is enforced, ranging from ‘despotic’ to ‘tolerant’) is a fundamental component of social relationships across primate species, but is poorly understood outside the macaque genus. Amongst our closest living relatives, bonobos are traditionally viewed as more tolerant than chimpanzees, but this is rarely empirically examined. Using observational data across five groups (1 wild; 4 captive) of each species, we assessed the co-variation of seven dominance style measures, and examined intra- and inter-species variation. In our principal components analyses, we found a single dominance style construct in chimpanzees (N=77), but measures were split across two components in bonobos (N=54). This suggests that the macaque dominance style framework maps more readily onto chimpanzees than bonobos. We found no evidence that either species differed in any individual dominance style measure, contradicting the narrative that bonobos are more tolerant than chimpanzees. Rather, we found considerable intra-species variation in dominance style, particularly in chimpanzees. We found that Western chimpanzees were more tolerant than other sub-species, and that chimpanzee male-male relationships were more tolerant than female-female relationships. Preliminary evidence also suggests that chimpanzees may be more tolerant in captivity than the wild, while bonobos may be more tolerant in the wild than captivity. Our results show how dominance style can be best measured among chimpanzees and bonobos and demonstrate that in our two closest relatives dominance style varies more within than between species.

Introduction

As outlined in chapter 1, dimensions of social structure vary widely across primate species, and in order to understand many important behaviours such as communication, co-operation and social cognition, it is crucial to achieve a solid understanding of the social context in which they evolve. One rather neglected aspect of social structure and relationships is dominance style. Variation in dominance style across and within primate species is not only interesting in itself, but has been found to explain variation in such variables as communication, cooperation and inhibitory control (Dobson, 2012; Joly et al., 2017;

Maestripieri, 1999; de Marco et al., 2019). Despite its predictive value and clear importance in determining social interactions, dominance style is rarely quantified outside the macaque genus. Primate species are often descriptively referred to as ‘tolerant’ or ‘despotic’ based on potentially subjective impressions of their behaviour. While the quantitative behavioural measures proposed by Thierry (200) provide a valuable starting point for assessing the dominance style of species across the primate order, he cautions against assuming their co-variation outside the macaque genus. Indeed, Bergstrom & Fedigan (2013) found that a group of white-faced capuchins displayed behaviours that would be considered a mix of despotic and tolerant in macaques. Similarly, in chapter 2 we examined 26 primate species (including many non-macaque species) and found that different dominance style variables predicted communication variables differently, indicating that they may not represent a single construct in all species. It is necessary to explicitly examine the co-variation of behavioural measures within each species to assess their dominance style, and to confirm whether they represent a single construct, or comprise multiple underlying components.

The dominance style of chimpanzees and bonobos, the closest relatives to humans and valuable models for understanding human evolution, is currently under debate. As outlined in chapter 1, bonobos are often described as being more tolerant than chimpanzees but more recently this traditional narrative is being challenged (e.g., Stevens et al., 2007). The term “tolerant” is also used inconsistently in the literature. A number of dyadic feeding experiments indicate that bonobos share food with others, including strangers, and also co-feed more than chimpanzees (Hare & Kwetuenda, 2010; Hare et al., 2007; Tan & Hare, 2013). This tendency to be in close proximity around valued resource is often described as an indication of greater tolerance (Cronin et al., 2014). However, empirical findings are not all supportive of this species difference, with two group-level feeding experiments actually indicating less food sharing and feeding proximity in bonobos compared to chimpanzees (eg., Cronin, De Groot, & Stevens, 2015; Jaeggi, Stevens, & Van Schaik, 2010). Importantly, feeding proximity is not one of Thierry’s (2000) proposed measures of dominance style, so whether it forms part of the dominance style construct in chimpanzees and bonobos remains an empirical question. Findings based on Thierry’s (2000) dominance style measures also provide a mixed account of whether bonobos are more tolerant than chimpanzees. Unlike chimpanzees, high intensity aggression is reported to be low in wild bonobos, and to date has never been reported to escalate to a fatality (Furuichi, 1997; Hare et al., 2012; Gruber & Clay, 2016). However, studies examining aggression directionality, hierarchy steepness and linearity in multiple captive groups suggest that bonobos could best be categorised as ‘semi-despotic’, and sometimes more despotic than chimpanzees (Stevens et al., 2007; Jaeggi et al., 2010). Similarly, Palagi, Paoli & Tarli (2004) found that reconciliation was significantly lower in a captive bonobo group compared to a captive chimpanzee group, again indicating relatively less tolerance in bonobos. Studies such as these challenge the traditional narrative that bonobos are highly tolerant compared to chimpanzees.

It is difficult to conclusively determine or compare the dominance style of *Pan* species from the available evidence for a number of reasons. Firstly, as discussed in chapter 1, studies that focus on a single group of chimpanzees or bonobos are insufficient for characterising the species, as there may be considerable intra-species variation in a given dominance style trait. It seems likely that there may be marked differences between wild and captive bonobo groups in particular, as the majority of studies indicating despotism in bonobos are from captive samples (eg., Cronin et al., 2015; Jaeggi et al., 2010; Palagi et al., 2004; Stevens et al., 2007) while those indicating tolerance are typically from wild or free-ranging sanctuary samples (eg., Furuichi, 1997; Hare et al., 2012; Hare et al., 2007). There may also be variation among sub-species of chimpanzees, as while the majority of chimpanzee research is focused on Eastern chimpanzees (*Pan troglodytes schweinfurthii*), other sub-species such as Western chimpanzees (*Pan troglodytes verus*), may have considerable differences in social behaviour (Gruber & Clay, 2016, Lehmann & Boesch, 2009). Secondly, most studies do not consider sex differences in dominance style, though some indicate this may be an important factor. For instance, male hierarchies were steeper than female hierarchies in Stevens et al.'s (2007) study with captive bonobos. Finally, and most fundamentally, dominance style measures have not yet been validated in chimpanzees or bonobos. We currently don't have evidence to suggest that the same measures that co-vary in macaques do so in *Pan*, or represent the same underlying construct of dominance style. In order to adequately assess and compare dominance style measures in *Pan,* it is necessary to examine multiple groups of chimpanzees and bonobos using comparable methods and assess covariation in a range of different behavioural measures.

The current study aimed to assess dominance style across multiple groups of chimpanzees and bonobos, including both wild and captive groups. We examined covariation in a range of observational behavioural measures to indicate which, if any, represent a single cohesive construct of dominance style in both species. Following Thierry (1990), de Waal (1991) and Castles et al., (1996) we examined this covariation at the intra-specific level. This allowed us both to examine whether the dominance style framework as applied to macaques also applies to *Pan,* and to create a behavioural index for use in future studies related to dominance style. If the dominance style measures in macaques also apply to *Pan* species*,* we would expect a principle components analysis to extract a single component where measures load in the expected direction (eg., high counteraggression but low intensity aggression). We also included two sociality measures; grooming rate and proximity. While we expect these to load most strongly on a separate component to dominance style, we expect them to load positively but weakly on the dominance style component. This is because although dominance style is separable from general sociality, affiliative interactions with others may be more important in gaining status, food, and mating opportunities within tolerant compared to within despotic relationships (Barret, Henzi & Lusseau, 2012; Foster et al., 2009; Patzelt, Pirow & Fisher, 2009).

We also measured the steepness and linearity of hierarchies, and descriptively examined how these related to the dominance style components. A steep and linear hierarchy is thought to form part of a despotic dominance style (eg., Balasumbramanian et al., 2012), but steepness of the hierarchy and dominance style may be quite different conceptually. Arguably, hierarchy steepness and linearity indicate differences in actual power, while dominance style captures the degree to which dominant partners enforce their power. We aimed to provide a preliminary test of whether despotic groups also have steeper and more linear hierarchies.

After forming dominance style component indices in chimpanzees and bonobos, we examined whether dominance style varied between species, groups and sexes, between wild and captivity, and between Western chimpanzees and other chimpanzee sub-species. This represents the most comprehensive assessment and comparison of dominance style in *Pan* to date, and provides valuable contribution to debates surrounding whether bonobos are the more tolerant of the two species.

Methods

Study Site and Subjects

The study included five groups of chimpanzees (N individuals = 77) and five groups of bonobos (N individuals = 54). The sample included only individuals independent of their mothers, which we defined as no longer depending on the mother for food, and no longer maintaining close proximity with the mother the majority of the time. Such subjects were chosen as they could form dominance relationships with other group members. Table 6 shows important details about all groups. Appendix 10 provides the sex, date of birth, sub-species and rearing history of all subjects.

Table 6

Details of all groups in sample.

Species	Site and Location	Wild or Captive	Enclosure/ Range Size	N of independent individuals included in sample
Chimpanzees	Budongo Trail, Edinburgh Zoo, Scotland	Captive	Indoor: 423m^2 Outdoor: 1832m^2	18
	Wolfgang Köhler Research Center, Leipzig Zoo, Germany (Group A)	Captive	Indoor: 430m^2 Outdoor: 4000m^2	17
	Wolfgang Köhler Research Center, Leipzig Zoo, Germany (Group B)	Captive	Indoor: 175m^2 Outdoor: 1400m^2	6
	Vallée des Singes Primate Park, Romagne, France	Captive	Indoor: 220m^2 Outdoor: 7500m^2	7
	Kanyawara Chimpanzee Project, Kanyawara, Uganda	Wild	~15-30 km2	29
Bonobos	San Diego Zoo, San Diego, United States of America	Captive	Indoor: 296m^2 Outdoor: 560m^2	8
	Wolfgang Köhler Research Center, Leipzig Zoo, Germany	Captive	Indoor: 256m^2 Outdoor: 2300m^2	8
	Vallée des Singes Primate Park, Romagne, France (Group A)	Captive	Indoor: 600m^2 Outdoor: 8000m^2	13
	Vallée des Singes Primate Park, Romagne, France (Group B)	Captive	Indoor: 600m^2 Outdoor: 3500m^2	6
	Lui Kotale, Salonga National Park, Democratic Republic of Congo	Wild	<15km	19

All captive group were free to roam in their outdoor or indoor enclosures (weather dependent) during the day which provided climbing frames, natural vegetation and enrichment, with all groups from Leipzig Zoo additionally participating in ongoing research experiments in the morning. All captive groups were fed a diet consisting mainly of vegetables and fruit and could forage for natural vegetation outside. Food was often pre-scattered prior to their release in their enclosure, and they are also fed regularly during the day. During feeds, food pieces were thrown by keepers in such a way that all individuals have access to food.

Equipment

Focal and aggression data at Leipzig Zoo and Vallée des Singes, and focal videos (used for proximity data) at Kanywara, were recorded with a Panasonic HDC-SD90 camcorder, with a Sennheiser MKE 400 microphone attached. Grooming and scan data at Leipzig Zoo and Vallée des Singes were recorded using an Olympus Digital Voice Recorder WS-853 and transferred to Excel sheets. Focal and aggression data were recorded at San Diego zoo using two Panasonic HC-V770 camcorders with two external Sennheiser MKE 400 unidirectional microphones. Proximity, grooming and aggression data were collected using individual coding sheets, created with the software FileMaker Pro (v.15.0.3.305), and then exported into Microsoft Excel sheets. Data from LuiKotale were collected using a mixture of voice audio recordings and written records using an IPAQ and paper and pen. All other data were recorded with pen and paper.

Ethical Note

This study complied with the ASAB/ABS guidelines for the use of animals in research and was granted ethical approval by the Biology Ethics Committee, University of York. Data collection was approved by the relevant authorities and ethical bodies (see appendix 11).

Data Collection

Observational data on grooming, aggression, reconciliation and proximity were collected, considering only interactions between individuals independent of their mother. Data were collected between April-August 2017 in Leipzig Zoo, July-September 2018 in Vallée des Singes, January-March 2017 in San Diego Zoo, January-December 2003 in Edinburgh Zoo, June 2014-March 2015 in Kanyawara, and November 2013-March 2014 in Lui Kotale.

Grooming.

Grooming was recorded from focal observations in three groups (Kanyawara, San Diego and Lui Kotale) and on an all-occurrence basis in all other groups (Altmann,1974). For all grooming bouts the identities and roles of the givers and receivers of grooming were recorded and whether roles were reversed during the grooming bout (ie., the initial giver became the receiver). A grooming bout was defined as all grooming behaviour within a dyad with pauses no longer than 3 minutes. All role reversals were considered part of the same bout.

Aggression.

Aggression data were recorded on an all-occurrence basis in all groups. Focal observations were paused to focus on aggression whenever it occurred. The identities of the aggressor and victim of the aggression were recorded along with the type of aggressive behaviour and whether the victim retaliated where possible. Table 7 indicates the ethogram of aggression types; one of these behaviours was considered aggression if accompanied by an aggressive posture or vocalisation by the aggressor, or submission, fleeing or retaliation from the victim.

A bout of aggression was defined as all aggressive acts between a dyad within a time criterion (30 seconds for the Lui Kotale group, 1 minute for the Edinburgh group, and 3 minutes for all other groups). This definition meant that a polyadic conflict consisted of two or more bouts. The aggressor was the individual to initiate the aggressive bout and the victim was the individual to initially receive aggression from the aggressor. An aggressive bout was defined as high intensity if the aggressor used physical contact.

Table 7

Ethogram of types of aggression included in aggression measures

Aggression Type	Definition	High Intensity? (contains physical contact?)
Threat	Behaviour directed at victim which incuded one or more of the following components: Flailing or raising arms at victim without making contact, bipedal approach to victim, jerking movement of body or head towards victim, Jump, Clap, ground stamp, shaking objects or arms.	N
Charge/Chase	Running towards victim with or without pursuit	N
Slap/Hit/Punch	Making hard physical contact with hand on body part of victim	Y
Kick	Making hard physical contact with foot or leg on body part of victim	Y
Grab/Pull/Tug	Gripping body part of victim with hand	Y
Push	Pressing hand against victim to displace them	Y

Hit with object	Making hard physical contact with object on body part of victim	Y
Bite	Gripping body part of victim with teeth	Y
Trample	Stamping on body part of victim	Y
Injurious physical attack	Physical contact with victim that results in a visible injury to the victim.	Y

Reconciliation.

Data on reconciliation were collected on five groups [Leipzig Chimpanzees (Group A), Leipzig Bonobos, and all three Vallée des Singes groups]. The standard post-conflict, matched-control (PC-MC) method was used, which controls for baseline levels of affiliation (De Waal & Yoshihara, 1983). This involves comparing the latency of affiliative behaviour in the post-conflict period (PC) with that in a period not following any aggression (matched control; MC). Following dyadic aggression, the aggressor and victim were followed and video-recorded for 15 minutes (the PC). If one individual moved out of visibility, just the remaining visible individual was followed. If both the aggressor and the victim went out of sight, the PC was cut short. All affiliative interactions between the victim and aggressor were recorded (see table 8 for affiliative behaviours). In the case of polyadic interactions, the victim and aggressor were chosen based on the dyad with the fewest PC-MC pairs if possible, or else the last dyad in the conflict. Within a week of the PC, at the same time +-1hour, a 15-minute MC observation which included the original victim and aggressor was taken (the MC). The requirements of the MC were that no aggression could have occurred in the group 15 minute prior, and the victim and aggressor had to be within 30m of one another at the start of the MC. If these conditions could not be met within 1 week of the PC, the PC was disregarded.

Table 8

Affiliative Behaviours Recorded in PC-MC Observations.

Behaviour	**Description**
Grooming	Directed cleaning/touching/visual inspection of the recipient’s hair or skin
Contact-sitting	Sitting in physical contact with the recipient, i.e. contact of leg on their back
Touching	Any instantaneous soft touch to the recipients body, other than to their genitals, using any body part other than the actors genitals
Play	Individuals wrestle/run/jump/chase/tickle accompanied by play face and/or laughing
Kiss	Mouth-to-mouth contact
Embrace	Individual places one/both arms around the recipient’s body while facing the partner or in lateral position
Hold	Grasping/holding onto recipient’s body or hair with one or both hands. Generally when recipient is walking or standing
Pat	Pronounced tapping/patting contact onto recipients body using flat hand
Inspect	Visual and contact inspection of the recipients wound or injured body part, following a conflict
Contact peer	Approach close to peer at recipient, resulting in contact
Sociosexual Behaviours	Mount, Copulation, Genital Touch, Thrusting, Genital-genito rubbing, Masturbation of other

Note. Descriptions from Clay & de Waal, (2013, 2014); Farooqi & Koyama, (2016)

PC-MC pairs were coded as attracted, neutral, or dispersed. When affiliation between the victim and aggressor occurred earlier into the PC than in the MC, it was coded as an attracted pair (an indication of reconciliation). When it occurred earlier into the MC than in the PC, it was coded as a dispersed pair. When it did not occur in either the PC or the MC, or if it occurred in the same minute into the PC and MC, it was considered a neutral pair. Each dyad was given a Conciliatory Contact Tendency Score (CCT), which is calculated by subtracting the number of dispersed pairs from the number of attracted, and dividing this by the total number of pairs.

Observation Times

To calculate observation times for rates of all-occurrence behaviour, scans were taken every 15 minutes during observations of all Leipzig and Vallée des Singes groups, recording the identities of all individuals visible. The observation time for each individual could then be estimated by multiplying the total observation time by the proportion of scans in which the individual was visible. For all other groups, the total focal observation times were calculated.

Proximity

To calculate both feeding proximity and non-feeding proximity, the presence or absence of an independent individual within 1m was recorded during feeding and non-feeding contexts in all groups by collecting scan data, with some variation in how these were collected across groups. In all Leipzig and Vallée des Singes groups, 15-second scans were taken during their normal feeding sessions to record feeding proximity, and at randomly chosen times during the day outside feeding sessions to record non-feeding proximity. A new individual was targeted every 15 seconds (during and directly after food provision in the feeding sessions), recording whether or not an independent individual was within 1m. The order of individuals targeted was predetermined, and if the individual was not visible they were skipped. An attempt was made to target every individual twice during each session. To supplement these sessions, presence or absence of an independent individual within 1m was also recorded from scans taken every 5 minutes during focal observations in both feeding and non-feeding contexts. In all other groups, presence or absence of an independent individual within 1m was recorded from scans taken every 5 minutes (Lui Kotale and San Diego), 10 minutes (Edinburgh) or 15 minutes (Kanyawara) during focal observations in both feeding and non-feeding contexts. Each of these focal follows from which scan data were taken, and each of the designated scan sessions, could be considered an independent scan session, containing 1-13 scans for an individual. For each individual we found the percentage of scans the individual was within 1m of an independent individual for each independent scan session, and we calculated the average percentage from all independent scan sessions (5-88 per individual).

Measures

From the data collected we extracted seven measures of dominance style (see Table 9 for descriptions); Aggression Intensity, Counteraggression, Rate of (low-intensity) Aggression, Directional Inconsistency Index (DII) for Aggression and Grooming, Reconciliation and Feeding Proximity, with a higher value representing greater tolerance in all except Aggression Intensity. Groom DII was an exploratory, previously unused but potentially useful measure of dominance style. Greater grooming symmetry could indicate greater tolerance, as dominant primates tend to received more grooming than subordinates (Schino, 2001). All other dominance style measure have been used previously, primarily in macaques (Balasubramaniam et al., 2012; Thierry et al., 2000; de Waal & Luttrell, 1989), though we used rate of low-intensity aggression rather than of all aggression as previous studies have used, as we think that a high rate of low-intensity aggression indicates greater tolerance more precisely. Each dominance style measure, with the exception of feeding proximity, was calculated in two forms; one including interactions with all possible partners, and the other including only same-sex partners. Feeding proximity could only be calculated in one form (including interactions with all possible partners), as we only recorded the identity of the nearest neighbour within 1m, but could not rule out that there were additional individuals of a different sex also within 1m.

We also extracted two ‘general sociality’ measures; grooming rate and non-feeding proximity with a high value in both representing greater sociality or social bonding (Crockford et al., 2013; Lehmann et al., 2016; McComb & Semple, 2005; Silk, Cheney & Seyfarth, 2013). Inclusion of these two measures allow us to tease apart the dominance style construct from general sociality. If some of our dominance style measures appear to represent a single construct in either chimpanzees or bonobos, we expect these two measures to load positively onto this component, as tolerant individuals should also be more affiliative, but to load more strongly onto a separate component as general sociality should be distinguishable from the dominance style construct.

Table 9 outlines all measures extracted from the data. Each measure was calculated per individual. A minimum criterion of two aggressive bouts per individual was required for inclusion in intensity and counteraggression measures, and two bouts per dyad for inclusion in both directional inconsistency index (DII) measures. For proximity measures (feeding and non-feeding), a given focal observation or targeted proximity data collection session could include multiple scans of an individual. The percentage of scans with an individual within 1m was calculated per focal sample or session, and a minimum of 5 of these focal samples/sessions was required per individual to be included in proximity measures.

Appendix 12 indicates the sample sizes across groups and measures, and reasons for missing data.

Table 9

Descriptions of all measures extracted from data (calculated per individual) and whether they measure dominance style or general sociality. The column on the right indicates whether a high or low value in the variable is associated with greater tolerance.

Measure	Measure Type	Description	Direction of value associated with tolerance
Aggression Intensity	Dominance Style	The percentage of aggressive bouts as aggressor of high intensity (i.e., with physical contact).	Low
Counter-aggression	Dominance Style	The percentage of aggressive bouts as aggressor which received counteraggression	High
Rate Low Intensity Aggression	Dominance Style	The number of low intensity aggressive bouts (ie., with no physical contact) as aggressor per hour of observation.	High
DII of Aggression	Dominance Style	Measure of directionality of aggression; the percentage of all aggressive bouts that occurred in the least frequent direction within a dyad, with respect to which individual was the victim or aggressor of each bout. (de Waal, 1977; Rowell, 1966). DII score per individual is the average DII of all dyads including individual.	High
DII of Grooming	Dominance Style	Measure of directionality of grooming. The percentage of all grooming bouts within a dyad that occurred in the least frequent direction, with respect to who gave and who received grooming. DII score per individual is the average DII of all dyads including individual.	High

Reconciliation	Dominance Style	The average conciliatory contact tendency (CCT) of each dyad (score which compares latency of affiliative behaviour between aggressor and victim in post-conflict compared to match-control periods; de Waal & Yoshihara, 1983). Reconciliation score per individual is the average CCT of all dyads including individual.	High
Feeding Proximity	Dominance Style	The percentage of scans during a feeding context with an individual within 1m (percentage of scans calculated per focal/session, and average value of all focals/sessions found per individual)	High
Grooming Rate	General Sociality	The number of grooming bouts involving individual (either as giver or receiver) per hour of observation.	High*
Non-Feeding Proximity	General Sociality	The percentage of scans during a non-feeding context with an individual within 1m (percentage of scans calculated per focal/session, and average value of all focals/sessions found per individual).	High*

Note: *The general sociality measures do not measure dominance style, but as greater tolerance is associated with greater sociality, we would expect that the general sociality measure would show some positive correlation with tolerance.

Data Analysis

Assessment of Dominance Style Measures

To examine the co-variation of dominance style measures in chimpanzees and bonobos and to assess whether they represent a coherent construct, we conducted two Principle Components Analyses (PCA); one for each species, with the seven dominance style variables (the version including interactions with all partners) and two sociality variables. We chose PCAs instead of principle axis factor analyses as Kaiser-Meyer-Olkin (KMO) test values were low, and previous studies indicate that the resulting structures from the two techniques are almost identical (Velicer, 1977; Weiss et al., 2011; Weiss et al., 2006). We implemented PCAs using a varimax rotation in *R* (RStudio Team, 2018) using the psych package (Revelle, 2018). We inspected scree plots and used parallel analyses to determine the number of components to extract for each species (Horn, 1965). We assessed whether components emerging from the PCA could feasibly represent the dominance style construct based on the loadings of the dominance style measures. For a component to be labelled as a dominance style component, we required that all of the dominance style variables with an absolute loading value greater than 0.3 were in the expected direction (e.g., if counteraggression loads positively, aggression intensity should load negatively; see table 9). We expected sociality measures (grooming rate and non-feeding proximity) to load positively but weakly on the dominance style component.

Dominance Style Component Scores

We used the results of the PCAs to form dominance style component scores for individual chimpanzees and bonobos. Each component was ultimately extracted in two forms per individual; one including interactions with all partners, and one including interactions with same-sex partners. We first identified the relevant variables that seemed to represent dominance style in that species (i.e. variables with an absolute loading greater than three in the predicted direction on the component we labelled as representing dominance style, that did not load more highly on a different component). For each of these variables (e.g. counteraggression, aggression DII and aggression intensity) we then calculated two sets of values: one including interactions with all possible partners and one with only same-sex partners. We then standardised these values across all individual chimpanzees or bonobos, generating two z-scores for each individual (all interactions and same-sex interactions for each variable of interest). For example, the ‘same-sex’ version of counteraggression was calculated from the percentage of bouts directed towards same-sex victims where the victim retaliated, standardised across all individuals. Aggression intensity was reverse-scored to match the direction of other dominance style variables. Finally, to calculate the two versions of each dominance style component scores for each individual, we took the mean of the individual’s Z scores for the variables that comprise the component, using the all-partner version Z scores for the all-partner components score, and the same-sex version Z scores for the same-sex component score. For example, the ‘same-sex’ version of a dominance style component score with counteraggression, aggression DII and aggression intensity would be formed from the average of the Z scores of the same-sex versions of these measures. As we didn’t calculate same-sex versions of feeding proximity, we excluded this measure from the same-sex component scores.

Linearity and Steepness

We measured the hierarchical linearity and steepness of all groups in our sample, and examined whether they relate to the dominance style components. Linearity indicates the degree to which individuals in a group can be placed in a linear rank order, while steepness indicates the size of power difference between ranks; i.e., at the steepest gradient, one partner within a dyad wins 100% of conflicts, while at the most shallow gradient, both partners win 50% of the time (de Vries, 1995; de Vries et al., 2006). We examine these two hierarchy qualities at the group level.

Using fleeing as indication of losing a conflict (Vervaecke et al. 2000), we used SOCPROG in Matlab (Whitehead, 2009) to calculate hierarchy linearity and steepness values for each group. We used the h' index to measure hierarchical linearity for each group (the standard linearity index which corrects for the number of unknown relationships; de Vries, 1995). For the hierarchy steepness of each group we used the slope of the regression line through individuals' normalised David's score minus their dyadic dominance index corrected for chance of winning (Dij), plotted against their rank (see de Vries et al., 2006 for full calculation of these values). We also examined how hierarchical steepness and linearity related to dominance style component scores by plotting group values, though sample size of groups did not permit inferential tests of these relationships.

Inter-species comparison

To test whether chimpanzees and bonobos differ in dominance style traits, we conducted Generalised Linear Mixed Models (GLMM) using the *lme4* package (Bates, Maechler & Bolker, 2012) in *R*. We constructed a separate model for each dominance style measure that emerged as part of a dominance style component in our PCA for either chimpanzees or bonobos, entering the dominance style measure as a fixed effect. For all models we entered Group as a random effect, and Species as the outcome variable. We didn't choose to construct a single model with all dominance style measures as fixed effects, as individuals would require data for all measures for inclusion, and the sample size of such individuals was very low (21 bonobos, 19 chimpanzees). We used a binomial distribution with a logit link, and estimated parameters using Laplace approximation. The combined residuals were not significantly different from the residual degrees of freedom in any of our models, indicating that overdispersion was not an issue. We obtained P-values by likelihood ratio tests of each full model with the dominance style measure as a fixed effect against a model without the effect in question.

Intra-species comparison

To test whether dominance style differed across different groups of chimps or bonobos, we conducted one-way ANOVAs in SPSS. For chimpanzees, we conducted an ANOVA comparing mean values of the single dominance style component that emerged from the PCA across the five groups. For bonobos, we conducted two ANOVAs comparing mean values of both dominance style components that emerged from the PCA across the five groups. The data showed some deviation from normality, but ANOVAs have been shown to be robust to non-normality even when groups have small and unequal sample sizes (Blanca et al., 2017). However, where data violated the assumption of homogeneity of variance we report *Welch's F* as this performs well when sample sizes and variance are unequal across groups (Field, 2013; Welch, 1951). Where ANOVAs were significant at p<.05, we examined which if any groups had significantly different scores by performing post-doc tests which control for familywise error.

Dominance Style in Chimpanzee Sub-species

To test whether dominance style in Western chimpanzees differs to that of other chimpanzee sub-species, we constructed a GLMM in R. We restricted the sample to those in captivity in order to remove the confound of living conditions. In the model, we included sub-species as the outcome variable (categorical variable with two levels; Western chimpanzees and non-western chimpanzees (including Eastern, Central and Hybrid chimpanzees)), group as random effect, and dominance style component index (including all partners) as the fixed effect. We used a binomial distribution with a logit link, and estimated parameters using Laplace approximation. The combined residuals were not significantly different from the residual degrees of freedom in any of our models, indicating that overdispersion was not an issue. We obtained P-values by likelihood ratio tests of each full model with the dominance style component as a fixed effect against a model without the effect in question.

Wild vs. Captivity

To test whether dominance style differs in chimpanzees and bonobos depending on living conditions (wild vs. captivity), we conducted t-tests in R. We did not use GLMMs with group as a random effect as all wild individuals were in a single group in each species. As the sample sizes of captive and wild individuals were very different, we used three *Welch's* t-tests; one with chimpanzees comparing wild and captive individuals' dominance style component scores, and two with bonobos comparing wild and captive individuals' scores in both dominance style components ('relationship symmetry and value' and 'conflict style').

Male and Female Dominance Style

To examine whether dominance style differed among males compared to among females, we constructed GLMMs in R. We examined chimpanzees and bonobo separately, with one model for chimpanzees (with the same-sex dominance style component that emerged from the PCA) and two for bonobos (with the two same-sex dominance style components that emerged from the PCA). For all models we included sex as the outcome variable, group as a random effect, and same-sex dominance style component index as the fixed effect. We used a binomial distribution with a logit link, and estimated parameters using Laplace approximation. The combined residuals were not significantly different from the residual degrees of freedom in any of our models, indicating that overdispersion was not an issue. We obtained P-values by likelihood ratio tests of each full model with the dominance style component as a fixed effect against a model without the effect in question.

Results

Assessment of Dominance Style Measures

To assess the correlation between dominance style variables in chimpanzees and bonobos, and to form dominance style component scores, we conducted two PCAs; one for each species. Figure 5 displays the correlation matrix for all variables in chimpanzees, while figure 6 displays the same correlation matrix in bonobos.

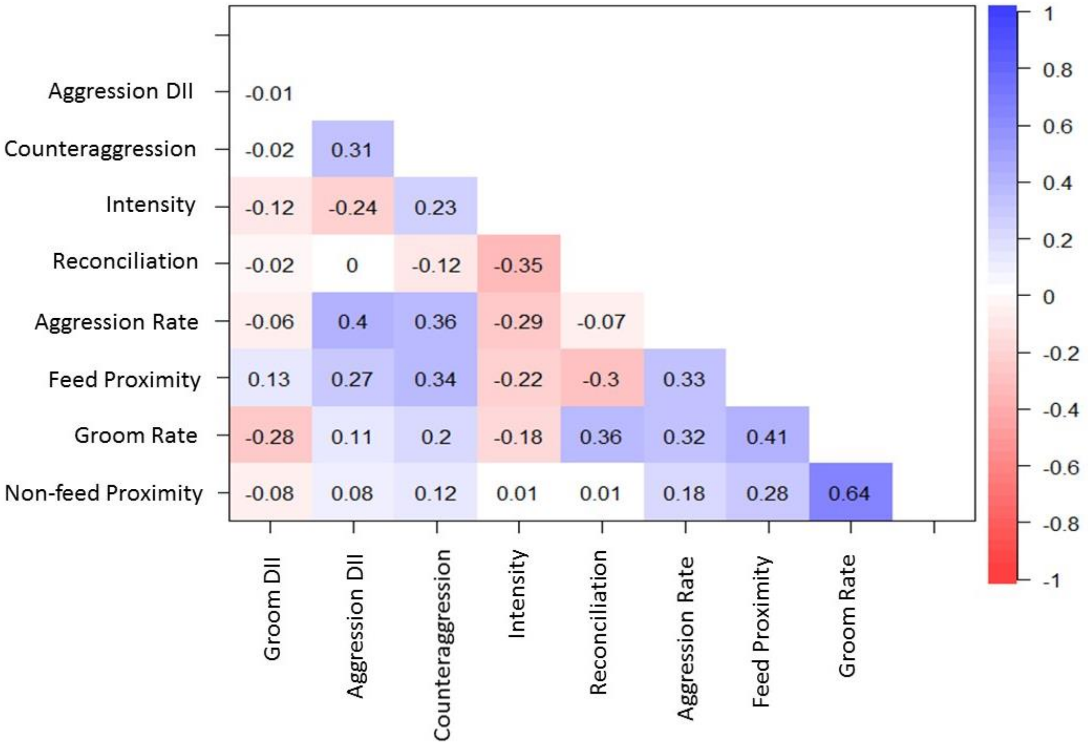


Figure 5 Correlation matrix of dominance style and sociality variables (including interactions with all partners) across all chimpanzees in the sample

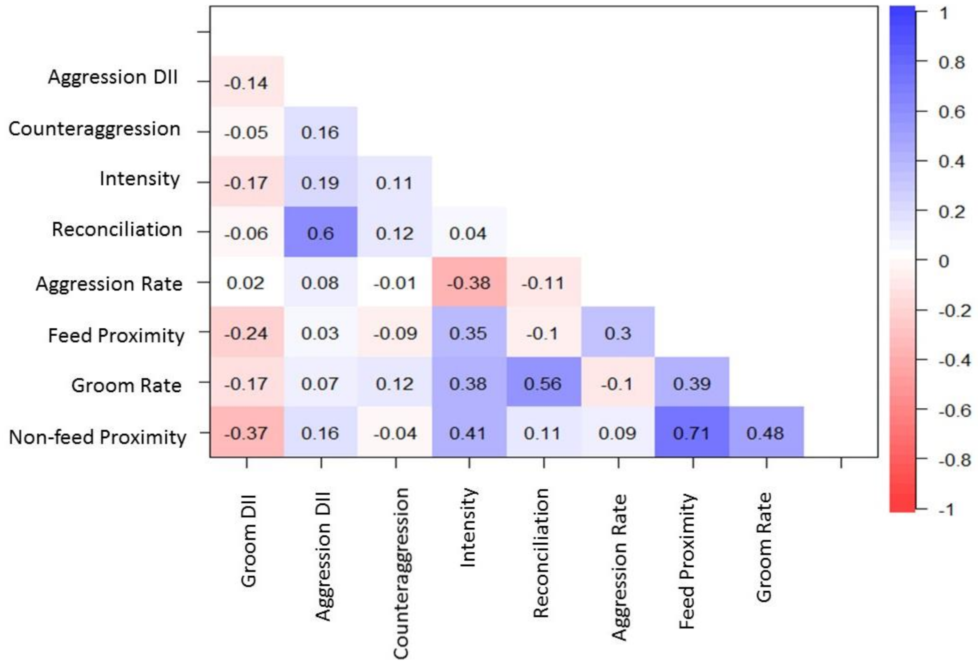


Figure 6 Correlation matrix of dominance style and sociality variables (including interactions with all partners) across all bonobos in the sample

Bartlett’s test of sphericity was highly significant for both species [Chimpanzees: χ2 (8) = 669.22, p<0.001. Bonobos: χ2(8)=170.98, p<.001], indicating that it was appropriate to conduct PCAs on the data. Examination of scree plots and parallel analyses indicated that three components should be retained for both species, and these components explain 62% of the variance for chimpanzees, and 64% for bonobos. Table 10 shows the component loadings of the variables on the components for chimpanzees and bonobos. The variable loadings indicate that for Chimpanzees, component 1 represents ‘dominance style’, component 2 represents “Sociability with grooming asymmetry”, and component 3 represents ‘Antagonistic tendency’. For Bonobos, component 1 represents ‘Sociability with grooming asymmetry and intense aggression, component 2 represents a ‘relationship symmetry and value’ aspect of dominance style, and component 3 represents a ‘conflict style’ aspect of dominance style. For all chimpanzees, dominance style component scores were calculated from the mean of Z scores for feeding proximity, rate of low intensity aggression, aggression DII and counteraggression. For bonobos, two dominance style component scores were calculated; one was calculated from the mean of Z scores for reconciliation, aggression DII and counteraggression, and the other was calculated from the mean of Z scores for rate of low intensity aggression and aggression intensity (with aggression intensity reversed scored first).

Table 10

Component loadings of the nine behavioural measures on the three components that emerged from a PCA in both chimpanzees and bonobos.

Chimpanzees

	Component 1 Dominance Style	Component 2	Component 3
Feeding Proximity	0.74	0.15	0.13
Rate Low Intensity Aggression	0.73	0.12	-0.10
Aggression DII	0.68	-0.10	-0.13
Counteraggression	0.56	0.18	0.44
Grooming Rate	0.32	0.84	-0.28
Non-Feeding Proximity	0.24	0.75	0.01
Groom DII	0.19	-0.56	-0.10
Intensity	-0.36	0.16	0.81
Reconciliation	-0.22	0.25	-0.77

	Bonobos		
	Component 1	**Component 2 Relationship Symmetry and Value**	**Component 3 Conflict Style**
Non-Feeding Proximity	0.89	0.04	0.00
Feeding Proximity	0.88	-.18	0.19
Grooming Rate	0.59	0.42	-0.27
Groom DII	-0.48	-0.07	0.03
Reconciliation	0.08	0.92	-0.05
Aggression DII	0.12	0.79	0.03
Counteraggression	-0.06	0.37	-0.12
Rate Low Intensity	0.17	-0.04	0.91
Aggression Intensity	0.53	0.06	-0.65

Note: Red text indicates variables with a higher absolute loading of 0.30. Yellow highlighted cell indicates variables included in a dominance style component score (which means the variable loaded most highly on that component, had a loading score above an absolute value of .3, and loaded in the expected direction for dominance style; see table 9)

Linearity and Steepness

We calculated the hierarchy steepness and linearity of all groups in our sample. Table 11 provides these values for male, female and overall hierarchies in each group. Descriptively, this shows chimpanzees and bonobos were similar in their overall steepness and linearity values, but values were higher for male and female hierarchies in bonobos compared to chimpanzees. This indicates that within the sexes, hierarchies were steeper and more linear in bonobos than in chimpanzees, but overall hierarchies were similar. In both species, and across almost all groups, male hierarchies were steeper and more linear than female hierarchies.

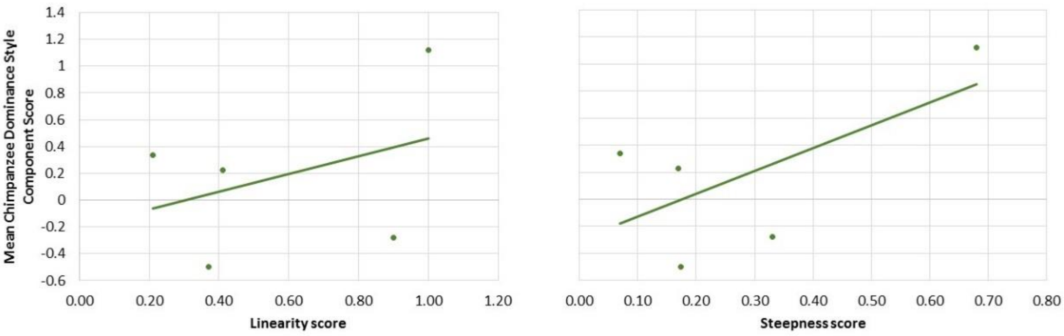
Figure 7 illustrates the relationships between the overall steepness and linearity scores and the overall dominance style component scores for chimpanzees and bonobos. These show that hierarchy steepness and linearity had a somewhat positive relationship with chimpanzee dominance style component score and bonobo component score 2 (relationship symmetry and value), but a negative relationship with bonobo component score 3 (conflict style). While we could only provide a descriptive account of these relationships, the positive relationships indicate that steep and linear hierarchies may not be associated with more despotic relationships as measured by our other behavioural dominance style measures.

Table 11

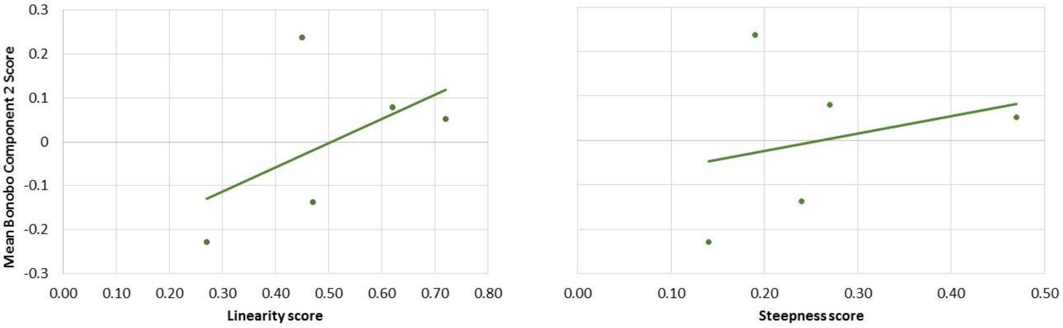
Hierarchy linearity and steepness scores across all chimpanzee and bonobo groups; separate calculations given for male, female and overall hierarchies. Linearity was calculated using the h' index (de Vries, 2005), and steepness was calculated using the slope of the regression line through individuals' normalised Davids' score minus their dyadic dominance index corrected for chance of winning (Dij), plotted against their rank (de Vries et al., 2006)

		Steepness			**Linearity**		
Species	**Group**	**Males**	**Females**	**Overall**	**Males**	**Females**	**Overall**
CHIMPANZEES	**Vallée des Singes**	0.57	0.44	0.68	1.00	1.00	1.00
	Edinburgh	0.18	0.04	0.07	0.41	0.39	0.21
	Leipzig (Group A)	0.32	0.09	0.17	0.45	0.44	0.41
	Leipzig (Group B)	NA	0.19	0.33	NA	0.80	0.90
	Kanyawara	0.32	0.09	0.17	0.55	0.26	0.37
	Mean	0.35	0.17	0.28	0.60	0.58	0.58
BONOBOS	**San Diego**	0.80	0.68	0.47	1.00	1.00	0.72
	Vallée des Singes (Group A)	0.36	0.25	0.24	0.60	0.68	0.47
	Vallée des Singes (Group B)	0.80	NA	0.27	1.00	NA	0.62
	Leipzig	NA	0.24	0.19	NA	0.90	0.45
	Lui Kotale	0.69	0.11	0.14	0.96	0.37	0.27
	Mean	0.66	0.32	0.26	0.89	0.74	0.51

a) Chimpanzee Dominance Style Score



b) Bonobo 'Relationship Symmetry and Value'



c) Bonobo 'Conflict Style'

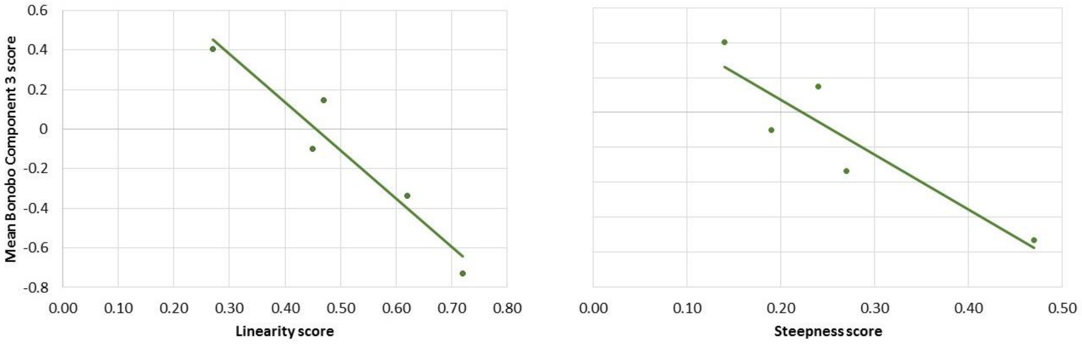


Figure 7 – Relationship between hierarchy linearity and steepness values and dominance style component scores across groups of chimpanzees and bonobos. Each data point represents value for one group; the mean value of the group is used for the component scores. Figure 7a) displays chimpanzee linearity (on the left) and steepness (on the right) against mean dominance style component score (aggression DII, counteraggression, feeding proximity and rate of low intensity aggression) across all chimpanzee groups. Figure 7b) displays bonobo linearity (on the left) and steepness (on the right) against mean component 2 score (representing relationship symmetry and value; aggression DII, counteraggression, and reconciliation) across all bonobo groups. Figure 7c) displays bonobo linearity (on the left) and steepness (on the right) against mean component 3 score (representing conflict style; rate of low intensity aggression and reverse-score aggression intensity). Linearity was calculated using the h' index (de Vries, 2005), and steepness was calculated using the slope of the regression line through individuals' normalised Davids' score minus their dyadic dominance index corrected for chance of winning (Dij), plotted against their rank (de Vries et al., 2006)

Inter-species Comparison

To test whether chimpanzees and bonobos differed in dominance style, we conducted six GLMMs, each with one of six dominance style measures as a fixed effect. The results from these models indicated that chimpanzees and bonobos showed no significant differences in Aggression DII, Counteraggression, Aggression Intensity, Feeding Proximity, Low Intensity Aggression Rate or Reconciliation (see table 12 for results of likelihood ratio tests and N of individuals included in each model). Our findings indicate that chimpanzees and bonobos do not differ in their degree of tolerance. Figure 8 indicates the mean scores across all measures for both species.

Table 12

Results of likelihood ration tests comparing 6 GLMMs with Species as the outcome variable, group as a random effect and a dominance style variable as a fixed effect, to a null model with no fixed effect.

Fixed Effect	**N individuals included in model**	**df**	X^2	***p***
Aggression DII	123	1	>0.001	0.976
Counteraggression	79	1	0.003	0.959
Aggression Intensity	109	1	0.015	0.903
Feeding Proximity	128	1	0.002	0.967
Rate Low Intensity Aggression	94	1	>.001	0.983
Reconciliation	46	1	>.001	0.987

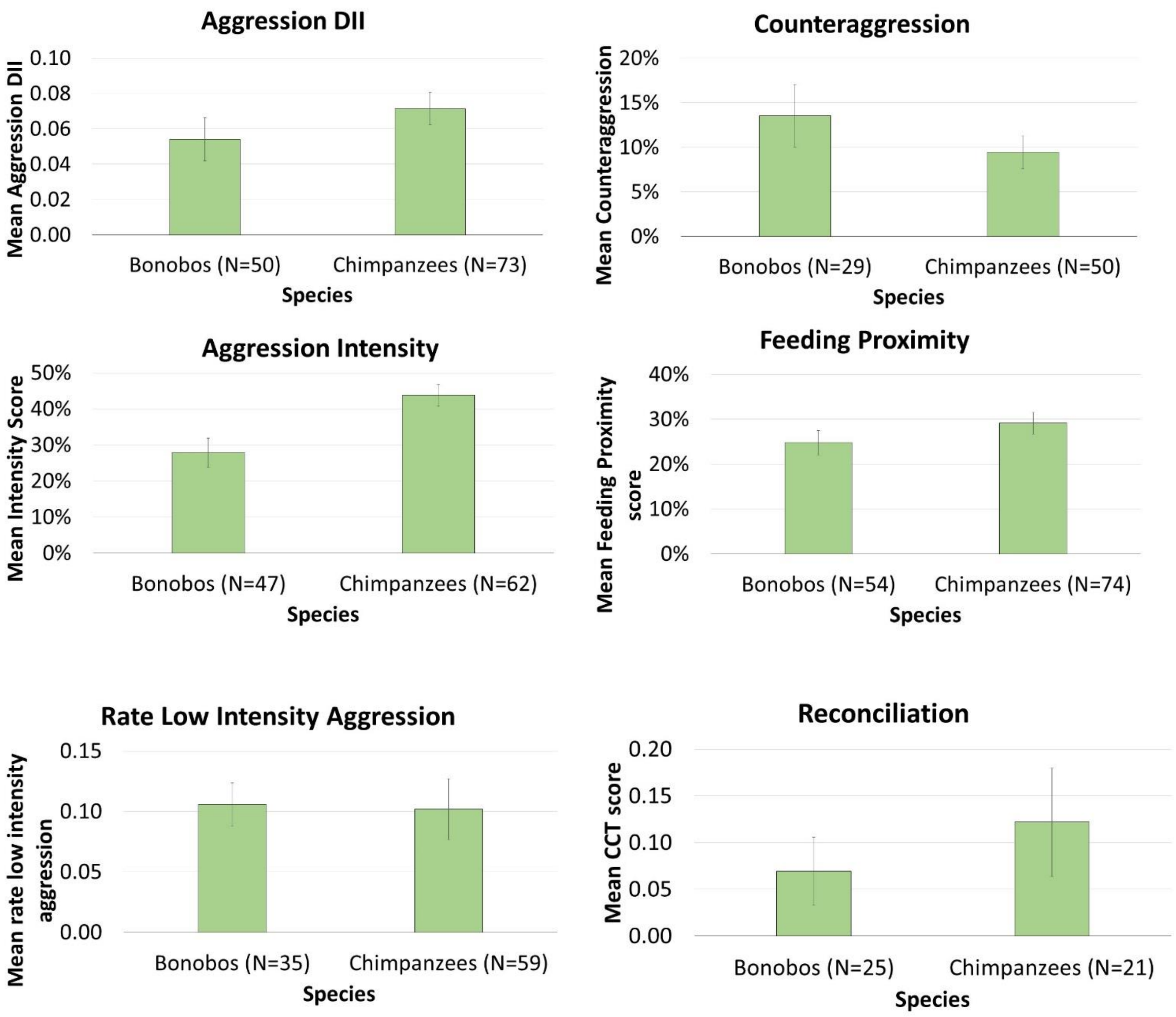


Figure 8 – The mean values of the six dominance style variables of chimpanzees and bonobos in our sample. Error bars represent standard error.

Intra-species comparison

Chimpanzees

To test whether groups of chimpanzees differed in dominance style, we conducted an ANOVA comparing group means of scores in the dominance style component that emerged from the chimpanzee PCA (component 1). Levene's test based on medians indicated that the variance of dominance style components were unequal across groups, F(4,72)=6.02, *p*<.001. The ANOVA indicated that chimpanzee groups differed significantly in dominance style component scores, *Welch's F*(4, 19.13) = 27.33 p<.001. We used *Games-Howell* post-hoc tests to compare groups as they control for multiple comparisons, and perform well when variances and sample sizes are unequal (Field, 2013). We found five pairwise comparisons to be significant. Figure 9 illustrates dominance style component scores across chimpanzee groups, and which groups were shown to differ significantly. Our results show that the chimpanzee groups in our sample exhibit considerable intra-species variation in dominance style.

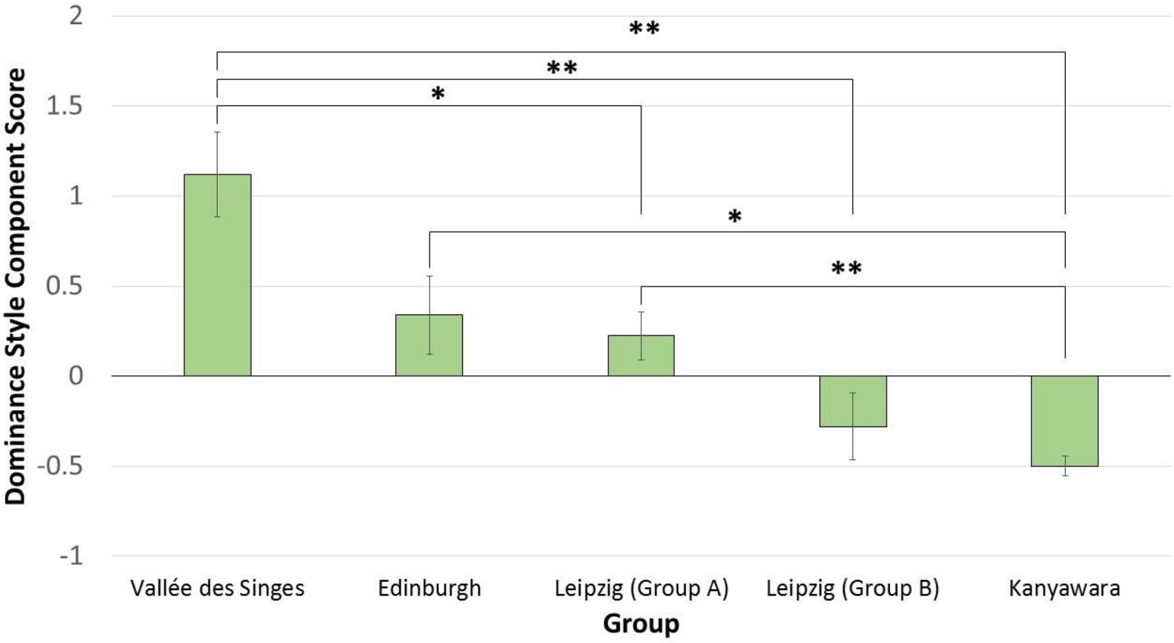


Figure 9 - Mean dominance style component scores across five chimpanzee groups. Dominance style component is formed from the means Z scores of Aggression DII, Counteraggression, Rate of Low Intensity Aggression and Feeding Proximity. Error bars represent standard error.
** Group means significantly different at p<.05 from Games-Howell post-hoc tests*
*** Group means significantly different at p<.001 from Games-Howell post-hoc tests.*

Bonobos

To test whether the bonobo groups differed in dominance style we conducted two one-way ANOVAs, comparing group means of scores in both dominance style components that emerged from the bonobo PCA (components 2 and 3). Levene's test based on median indicated that variances were equal across groups in both components; component 2, F(4, 46)=0.54, p=.705 component 3, F(4,48)=0.40, *p*=.811. The ANOVAs indicated that bonobo groups did not differ significantly in one dominance style component (component 2; representing relationship symmetry and value); F(4,46)=.54, *p*=.710; but did differ significantly in the other (component 3; representing conflict style); F(4,48) = 2.83, *p*=.035. To compare group means in component 3, we used Hochberg's GT2 post-hoc tests as they control for multiple comparisons and perform well when group sizes are different (Field, 2013). We found just one pairwise comparison to be significant. Figure 10 illustrates scores of both dominance style components across the five bonobo groups, and which groups were shown to differ significantly. Our results show that the bonobo groups in our sample exhibit low intra-species variation in dominance style; there is some variation in their 'conflict style' component of dominance style, but little variation in their 'relationship symmetry and value' component of dominance style.

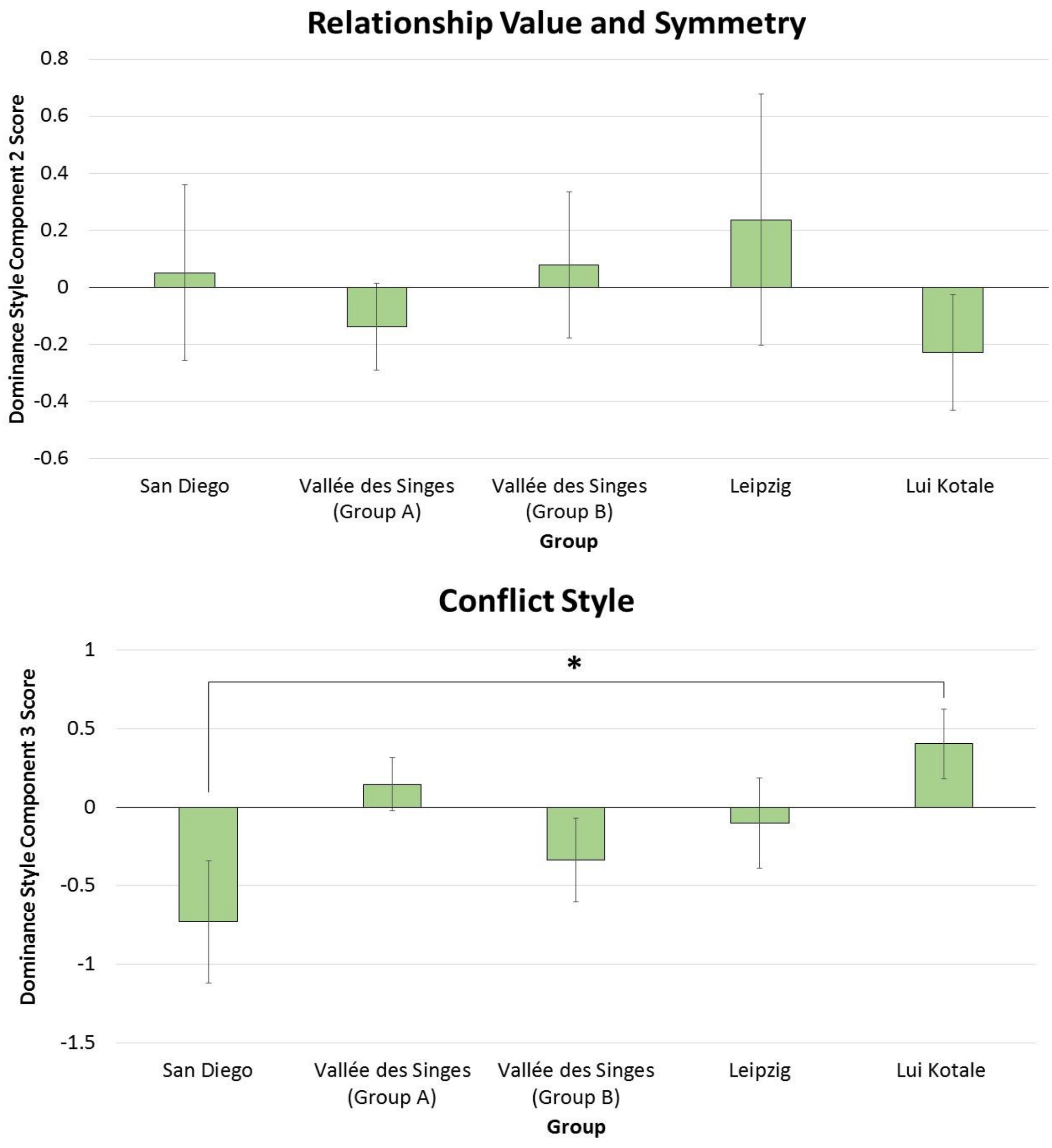


Figure 10 - Mean dominance style components scores across five bonobo groups. The top graph illustrates values of component 2, which represents the 'relationship symmetry and value' component of dominance style (mean Z scores of aggression DII, counteraggression and reconciliation), while the bottom graph illustrates values of component 3, which represents the 'conflict style' component of dominance style (mean Z scores of aggression intensity and rate of low intensity aggression). Error bars represent standard error
** Group means significantly different at p<.05 from Hochberg GT2 post-hoc tests*

Dominance Style in Chimpanzee Sub-species

To test whether dominance style in captive Western chimpanzees was different to that of other captive sub-species, we constructed a GLMM and compared it to a null model. The likelihood ratio test indicated that Western chimpanzees had a significantly higher dominance style component score than that of the other sub-species [$x^2(1)=4.12$, $p=.042$], as illustrated in figure 11. This indicates that Western chimpanzees are more tolerant than individuals of other sub-species.

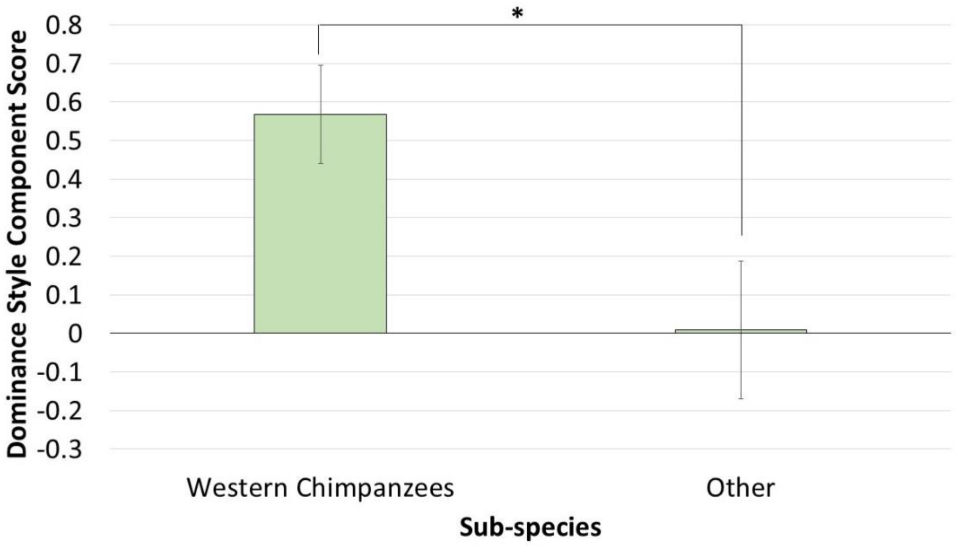


Figure 11 - Dominance Style component scores (including measures of counteraggression, aggression DII, rate of low intensity aggression and feeding proximity) of captive Western Chimpanzees (N = 28) compared to those of other captive sub-species (N = 20). Error bars represent standard error. Asterisk indicates p<.05.

Wild vs. Captivity

To test whether chimpanzee and bonobo dominance style differed depending on living conditions, we conducted three Welch's t-tests. The first t-test indicated that captive chimpanzees had a significantly higher dominance style component score than wild chimpanzees [*Welch's* $t(66.86) = -6.67$, $p<.001$]. This shows that the captive chimpanzees in our sample were more tolerant than their wild counterparts, as illustrated in Figure 12. The two t-tests with bonobos indicated that there was no difference between wild and captive individuals in the 'relationship symmetry and value' component [*Welch's* $t(31.58) = -1.038$, $p=.307$], but wild individuals had a significantly higher 'conflict style' component score than captive individuals [*Welch's* $t(30.88) = 2.26$, $p=0.031$], as illustrated in Figure 12. This shows that compared to captive individuals, the wild bonobos in our sample had a conflict style with more frequent but less intense aggression; potentially an indication of greater tolerance.

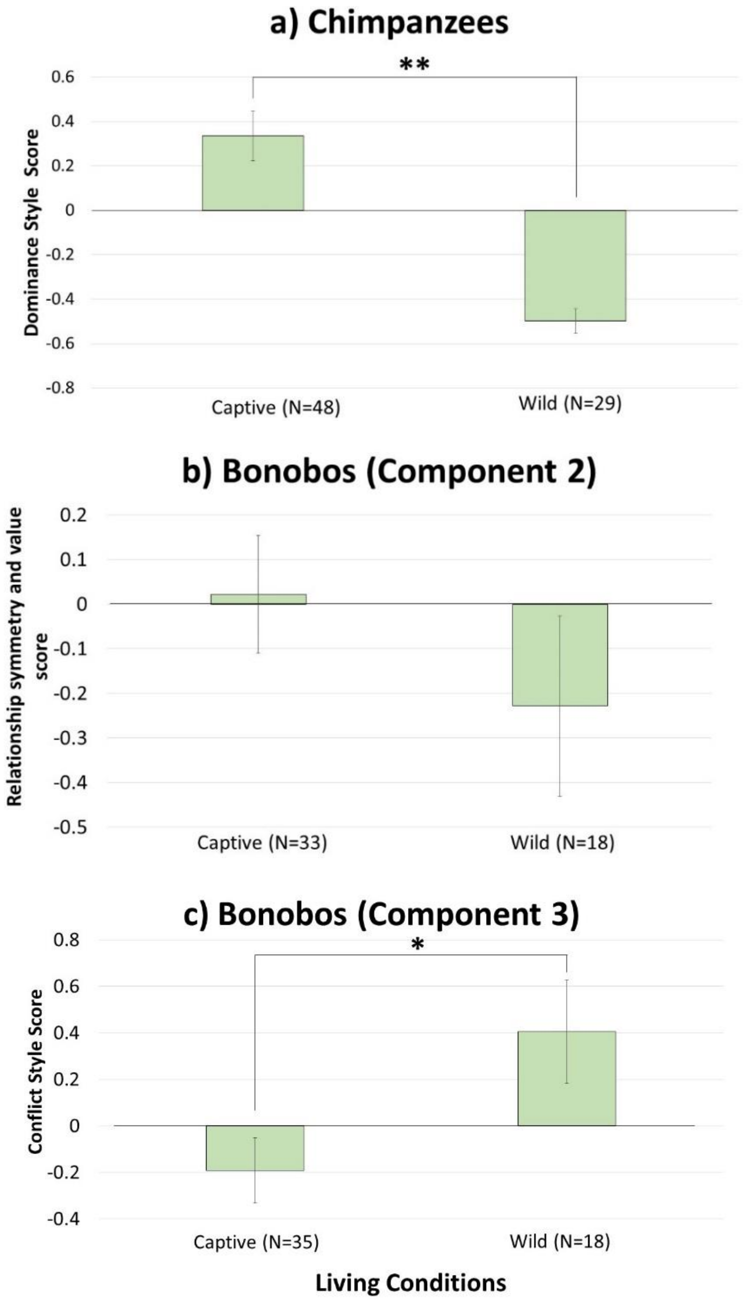


Figure 12- Comparison dominance style components in wild and captive individuals. Figure 12a) shows values of the dominance style component in chimpanzees, which includes measures of counteraggression, aggression DII, rate of low intensity aggression and feeding proximity. Figure 12b) shows values of component 2 in bonobos – 'relationship symmetry and value', which includes measures of counteraggression, aggression DII and reconciliation. Figure 12c) shows values of component 3 in bonobos – 'conflict style' which includes measures of rate of low intensity aggression and reverse-scored aggression intensity. Error bars represent standard error. Single asterisk indicates p<.05. Double asterisk indicates p<.001.

Male and Female Dominance Style

To test whether dominance style in same-sex relationships differed between males and females in chimpanzees and bonobos, we conducted three GLMMs (one including chimpanzees, two including bonobos). As indicated in table 13, our models indicated a significant sex difference in the chimpanzee dominance style component score, but none in either bonobo dominance style component score. Figure 13 shows that male chimpanzees are more tolerant than females in their same-sex relationships.

Table 13

Results of likelihood ration tests comparing 3 GLMMs with sex as the outcome variable, group as a random effect and one of the three same-sex dominance style component scores as a fixed effect, to a null model with no fixed effect.

Fixed Effect	**N individuals included in full model**	**df**	X^2	***p***
Chimpanzees same-sex dominance style component score	67	1	7.75	0.005
Bonobos same-sex dominance style component score 2 (Relationship value and symmetry)	45	1	0.05	.832
Bonobos same-sex dominance style component score 3 (conflict style)	35	1	0.19	.660

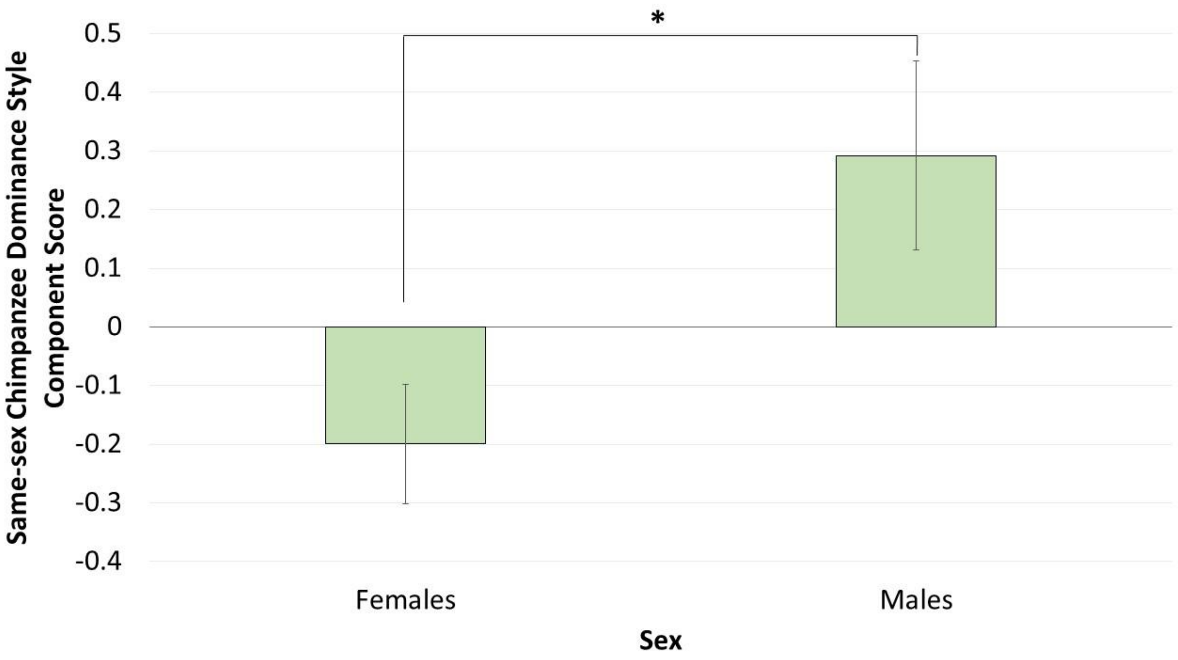


Figure 13 – Comparison of same-sex dominance style component score (formed from mean of Z scores for counteraggression, aggression DII and rate of low intensity aggression including same-sex partners only) in chimpanzees. Asterisk indicates p<.05

Discussion

The goal of this study was to examine dominance style in chimpanzees and bonobos. We assessed the covariation of multiple behavioural measures in each species, and found that they represented a single dominance style component in chimpanzees, but were split across two components in bonobos; ‘relationship symmetry and value’ and ‘conflict style’. This suggests that the dominance style framework based on macaque species appears to map readily onto chimpanzees, but may not in bonobos. Our results indicate that hierarchy linearity and steepness may be separate to the dominance style construct in *Pan.* From our analysis we created a dominance style index in chimpanzees, which can be used in future studies to test how dominance style relates to variables such as communication, cognition and brain size. We examined inter- and intra-species variation in dominance style traits, and found no evidence for consistent species differences in tolerance within *Pan*, but did find that dominance style varies across groups within the same species, particularly in chimpanzees. Notably, we found that Western chimpanzees were more tolerant than other sub-species, and that male-male relationships were more tolerant than female-female relationships in chimpanzees. We also provide preliminary evidence that chimpanzees may be more tolerant in captivity, while bonobos may be more tolerant in the wild. Our study represents the most comprehensive assessment of dominance style in *Pan* to date.

We found that, similar to macaques, there appears to be a single “dominance style” construct that explains patterns of behaviour in chimpanzees. Our results suggest that dominance style can be measured in chimpanzees by counteraggression, aggression symmetry, rate of low intensity aggression and feeding proximity. From these measures we were able to form a chimpanzee dominance style index, which can be used in future tests of hypotheses related to dominance style. The two dominance style measures that did not meet the criteria for inclusion in this index were reconciliation and aggression intensity, although aggression intensity did have a moderate loading on the component in the expected direction. These measures may therefore not be appropriate for measuring dominance style in chimpanzees. Grooming symmetry was an exploratory measure but does not appear to be related to dominance style in either chimpanzees or bonobos. Overall, our results indicate the macaque framework for dominance style applies to chimpanzees.

While our findings with chimpanzees suggest their dominance style can be understood similarly to that of macaque species, our findings with bonobos are less easily interpretable. We found that the dominance style construct comprises two separate underlying components in bonobos; ‘relationship symmetry and value’ (counteraggression, aggression DII and reconciliation) and ‘conflict style’ (rate of low intensity aggression and aggression intensity). This indicates that there may be two different facets of dominance style in bonobos. While dominance style is generally described in macaques as a behavioural suite incorporating both of these components (Thierry et al., 2008), this framework seemingly does not apply to bonobos. The ‘dominance style’ term was originally used to describe patterns of agonistic asymmetry rather than focusing on conflict management behaviours (Flack & de Waal, 2004; de Waal & Luttrell, 1989). Under this description, dominance style is best captured by the ‘relationship symmetry and value’ component in bonobos, which is supported by our finding that one sociality measure (grooming rate) loads positively on this component. Our findings may suggest that description of species’ dominance style should focus on symmetry of interactions, and it should not be assumed that other conflict management traits are related to the construct as they are in macaques. However, it is necessary to assess dominance style traits in a wide range of non-macaque species to confirm that the separation of these two components is not a peculiarity in bonobos. We also note that neither potential dominance style component explained the most variance in bonobos. The component that explained the most variance is difficult to interpret; it indicated that greater sociability (grooming rate and proximity) and feeding proximity was related to more asymmetrical grooming and higher intensity aggression. It could reflect that more general spatial cohesiveness is maintained through unidirectional grooming but also causes more intense aggression, but this component does not appear to reflect dominance style. Overall, we conclude that dominance style in bonobos is less easy to interpret and is different to that in chimpanzees and macaques, and as such we interpret our other analyses related to dominance style in bonobos with caution.

Our preliminary findings on hierarchical linearity and steepness suggest that it may be appropriate to separate these from the dominance style construct. In chimpanzees, we found a trend for groups with steeper and more linear hierarchies to be more tolerant (based on their dominance style component scores), and in bonobos, for such groups to have greater relationship symmetry and value. This runs counter to previous assertions that greater hierarchy steepness and linearity equates to greater despotism (e.g., Balasubramaniam et al., 2012; Stevens et al., 2007). We suggest that these two aspects of the hierarchy are conceptually different from the dominance style construct, in that they represent actual differences in dominance asymmetry, while dominance style represents the strictness with which dominance asymmetry is enforced. Indeed, dominant partners may only be willing to show tolerance to subordinates when their higher status is secure. Separating hierarchy linearity and steepness from the dominance style construct also helps to explain our findings comparing male and female hierarchies. Descriptively, we found that male hierarchies were more steep and linear than female hierarchies of both species, which is consistent with previous studies (e.g,. Newton-Fisher, 2004; Stevens et al., 2007). However, we found that based on dominance style component scores, male chimpanzees were significantly more tolerant amongst each other than were female chimpanzees, providing further support for our suggestion that well-established dominance asymmetry may permit greater tolerance. However, this may not be the case for all species. We found no sex difference in either of bonobos' potential dominance style components despite males having more linear and steeper hierarchies. Bonobo groups with more linear and steeper hierarchies had a more despotic 'conflict style', which is in line with hierarchical steepness and linearity being related to a more despotic dominance style in macaques (Balasubramaniam et al., 2012). Nonetheless, with the exception of this one finding, overall our results suggest that hierarchy steepness and linearity should not be assumed to form part of the dominance style construct in all species. Future research should examine the relationship between these variables in a larger sample of groups in each species.

Our findings contribute to growing evidence that bonobos may not be more tolerant than chimpanzees as is traditionally thought. There were no significant differences between chimpanzees and bonobos in any of their dominance style measures (aggression DII, counteraggression, aggression intensity, rate of low intensity aggression, feeding proximity). While previous studies provide a mixed account of whether chimpanzees or bonobos are more tolerant (eg., Cronin et al., 2015; Hare et al., 2007; Palagi et al., 2004), to our knowledge, this is the first study to directly compare multiple groups of both species across a range of dominance style measures. By doing so, we were able to account for intra-species variation in dominance style, which we found in both species and which could explain why we found no significant difference between them. We found particularly striking variation across chimpanzee groups, as well as between chimpanzee sub-species, and also found preliminary evidence of differences in dominance style in the wild compared to captivity. Descriptively, hierarchy steepness and linearity also appeared to vary more within compared to between species. These findings highlight that it is not possible to characterise a species based on observations of a single group, supporting Gruber & Clay's (2016) assertion that chimpanzees and bonobos should not be viewed as polar opposites, but rather fitting along a continuum. Indeed, even in macaque species which are typically categorised into a dominance style grade from 1-4, there is a lack of studies such as ours examining intra-species variation and co-variation of dominance style measures (but see Zhang et al., 2014). Doing so is necessary to assess whether it is appropriate to place a species into a dominance style grade, and to help to explain some findings that dominance style measures do not always co-vary in a linear fashion across macaque species (e.g., Balasubramaniam et al., 2012; Berman et al., 2004). On the whole, our findings indicate that neither chimpanzees nor bonobos can be universally described as more tolerant, though we cannot rule out that there may be consistent differences between both species in the wild, or between bonobos and particular chimpanzee sub-species.

The intra-species variation in dominance style we observed could be explained by our findings related to sub-species and living conditions. We found that the captive Western chimpanzees in our sample were more tolerant than their counterparts of other sub-species (Eastern, Central and hybrid of unknown combination). This could potentially underlie the variation in dominance style across our chimpanzee groups. This adds to evidence that Western chimpanzee social behaviour appears to be distinct from that of other sub-species (Gruber & Clay, 2016). Indeed, their greater tolerance could account for their reduced tendency to engage in lethal aggression in the wild compared to Eastern chimpanzees (Wilson et al., 2014). We focused on captive groups only in these analyses, to remove the confound of captive vs. wild conditions. The fact that many of these Western chimpanzees live in captivity among individuals of other sub-species points towards an inherited basis of dominance style, which is consistent with previous studies showing a phylogenetic signal in macaque dominance style traits (Balasubramabiam et al., 2012). We found some preliminary evidence that chimpanzees are more tolerant in captivity, while bonobos may be more tolerant in the wild. However, the conclusions we can draw from these findings are limited for a few reasons. Firstly, in bonobos, we only found a difference between wild and captivity in one of the two potential dominance style components. We have shown that wild bonobos have a conflict style involving more frequent but less intense aggression compared to captive bonobos. Secondly, we only have one wild group compared to four captive groups in each species. Finally, while the captive chimpanzee groups combined were more tolerant than the wild group, it is uncertain whether this was due to living conditions or because of their sub-species composition; the majority of captive individuals were either Western chimpanzees or a hybrid (potentially including Western chimpanzee), while all wild individuals were Eastern chimpanzees. Future studies should compare multiple captive and wild groups of the same sub-species.

In this study we have provided the most comprehensive assessment of dominance style in chimpanzees and bonobos to date. Our analyses provide an empirical basis for using similar behavioural measures to measure dominance style in chimpanzees as in macaques, and we provide a chimpanzee dominance style index for use in future studies. However, our analysis of dominance style measures in bonobos was less easily interpretable. From our observations of multiple groups in both species, we found no evidence that chimpanzees and bonobos differ in any dominance style measure. However, as the majority of our sample was in captivity, and we found preliminary evidence of differences in dominance style in captivity compared to in the wild, we suggest that future research examine whether the two species differ in a wild context. We found considerable intra-species variation in dominance style, especially in chimpanzees, and provide the first empirical evidence that Western chimpanzees are more tolerant than other chimpanzee sub-species. For this reason, we also suggest that future research examine whether dominance style differs between bonobos and specific sub-species of chimpanzee. Additionally, while we found no sex differences in bonobo dominance style relating to same-sex interactions, in chimpanzees we found greater tolerance in male hierarchies compared to female hierarchies. Taken together, our findings provide a valuable contribution for understanding the social structure of our closest relatives.

Chapter 4: Dominance style and individual communicative strategies in *Pan*: a multimodal approach

Abstract

Chimpanzees and bonobos exhibit impressive communicative abilities, but how the communicative strategies of these species compare to each other and in relation to social variables is poorly understood. Here I provide a descriptive overview of communication in six captive groups of *Pan* using a multimodal approach, and test the degree to which variation in individual communicative strategies is predicted by dominance style (the strictness with which dominance is enforced, ranging from 'despotic' to 'tolerant'). By examining a range of different communication measures, I found that chimpanzees tended to use more frequent and elaborate communication than bonobos, but both species showed relatively low rates of multimodal compared to unimodal communication. I found that bonobos who were more tolerant to lower-ranking partners, and chimpanzees who received more tolerance from higher-ranking partners, displayed more frequent and elaborate communication. These findings show that dominance style is an important predictor of individual communication strategies, though this relationship differs even between closely related species.

Introduction

There exists rich variation across multiple facets of primate communication, and the factors associated with such variation has attracted widespread research interest. Investigating these factors can shed light on the evolution of communication, which in turn can provide insight into the evolution of cognitive abilities, as well as informing theories of human language (Dunbar, 1988; 1993; Zuberbühler, 2005). Typically, such research focuses on variation in innate communicative repertoires, which has been found to be associated with variables such as group size, dominance style and cortical measures (Chapter 2; Dobson, 2012; Dunn & Smaers, 2018; McComb & Semple, 2005). These findings are valuable for understanding how communication systems evolve over evolutionary time, but do not capture individual variation in the use of these systems. Individual primates may vary in their use of the signals in their inherited repertoires, such as in the frequency or combination of signals, or use of signals to achieve goals, but this is often neglected in the literature. Focusing on such variables related to communication use and complexity at the individual level can provide insight into the factors that drive the evolution of communication systems at the phylogenetic level. Only by studying variation in individuals' communicative strategies can we fully appreciate the capacity and complexity of a species communication system.

In order to capture the full extent of primate communicative strategies, a multimodal approach is essential. Most studies in primate communication focus on just one of vocalisations, gestures or facial expressions, but researchers are increasingly acknowledging the importance of using the same methods to study communication from multiple modalities at the same time (Liebel et al., 2013; Frohlich & van Schaik, 2018; Slocombe, Waller & Liebel, 2011; Waller et al., 2013). Liebel et al., (2013) argued that applying different methods to researching different modalities creates a bias in the literature, skewing our understanding of what capacities underlie gestures, vocalisations and facial expressions. In terms of communicative strategies, they argued that studying just one modality at a time fails to capture the complexity associated with combining signals from different modalities during a communicative interaction. Moreover, in the face of an unresponsive partner, an individual may elaborate with signals from a different modality in pursuit of a social goal, which can only be captured with a multimodal approach. Even the true rate of communicating is obscured by unimodal approaches; an individual may appear to communicate infrequently when considering just vocalisations for instance, but could in fact communicate more frequently than others when considering vocalisations, gestures and facial expressions together. Overall, a multimodal approach can capture aspects of primate communicative strategies that are not possible with unimodal methods.

Chimpanzees and bonobos are closely related species with relatively similar communication systems, including innate repertoires across multiple modalities; primarily vocal, gestural and facial repertoires (Graham, Furuichi & Byrne, 2017; Hobaiter & Byrne, 2011; Parr, Waller, Vick & Bard, 2007; Slocombe & Zuberbühler, 2010; de Waal, 1988). As discussed in chapter 1, they use these repertoires in elaborate ways, including combining signals into sequences (signals produced one after the other; Tomasello et al., 1994), multimodal signals (signals from different modalities produced with temporal overlap; Waller, Liebal, Burrows, and Slocombe, 2013) and using signals to pursue social goals (Clay & Zuberbuhler, 2011; Genty, Neumann & Zuberbuhler, 2015; Graham, Furuichi & Byrne, 2017; Liebal, Call & Tomasello, 2004; Wilke et al., 2017). Using a multimodal approach, the natural communication of chimpanzees has been more closely examined compared to that of bonobos. Wilke et al., (2017) and Hobaiter et al., (2017) provide a comprehensive assessment of the use of unimodal and multimodal signals in wild chimpanzees, including response rates, persistence and use across contexts. Taglialatela et al., (2015) focused on vocalisations in captive chimpanzees and found that they were produced alongside signals from other modalities fifty percent of the time. Despite their close phylogenetic relationship, the communicative strategies of chimpanzees and bonobos are rarely compared. Pollick & de Waal (2007) provide an overview of the use and context-specificity of different modalities in captive chimpanzees and bonobos, and examined responsiveness to unimodal and multimodal signals (although their definition of multimodal allowed gaps of up to 10 seconds between signals). In this chapter I provide an overview of a wider range of communication measures in captive chimpanzees and bonobos using a multimodal approach, and test how individuals' communicative strategies relate to their dominance style.

There are many reasons why dominance style is likely to predict communication as outlined in chapter 1. In chapter 2 we found that greater tolerance was associated with a higher vocal rate across a wide range of primate species, suggesting a link between dominance style and individual communicative strategies. A more in-depth and multimodal assessment of communication strategies can more comprehensively assess how dominance style is related to communication, and can provide further insight into potential reasons for their linkage. For instance, one potential reason is that tolerant individuals may face greater pressure to use communication to achieve goals in lieu of threat of force, so focusing specifically on goal-oriented communication can help to uncover whether this is a likely explanation for their linkage. By using a multimodal approach it is possible to capture greater complexity in communicative strategies and to test whether this is related to the more socially complex tolerant dominance style, as predicted by the social complexity hypothesis (Freeberg et al., 2012).

In the current study I aimed to provide a comprehensive assessment of communicative strategies in captive chimpanzees and bonobos using a multimodal approach (for bonobos, the most comprehensive to date), and to compare this to previous literature. Subsequently, I aimed to test whether dominance style predicts individual variation in these strategies in chimpanzees and bonobos. Chapter 3 established dominance style indices for both species, providing quantifiable measure of dominance style per individual. Here I measured 'given tolerance' and 'received tolerance' separately as done in chapter 2 using these established dominance style indices. This allowed me to test whether the tolerance a dominant individual shows to lower-ranking partners, or the tolerance a subordinate individual receives from higher-ranking partners, predicts aspects of communicative strategies.

I focused here primarily on five aspects of communicative strategies; the rate of signalling overall, the rate of goal-oriented communication, persistence and elaboration, signal sequences and multimodal sequences. The multimodal approach allowed me to more closely capture the true rate of an individual's signalling, which indicates their tendency to communicate overall. By also measuring the rate of communicative interactions that are directed towards a goal, and persistence and elaboration in the face of an unresponsive partner, I could provide evidence as to whether the link between dominance style and communication is related to an increased need to communicate to achieve goals. The inclusion of multimodal signals and signal sequences provide potential indications of complexity in communicative strategies, as they are comprised of multiple components allowing opportunity for additional information to be transmitted (although there is much debate as to what kinds of communication can be considered more ‘complex’; eg,. Peckre, Kappeler & Fichtel, 2019). While previous research indicates that combining vocalisations into sequences may provide receivers with additional information (Clay & Zuberbuhler, 2011; Crockford & Boesch, 2005), there is evidence that some gesture sequences may indicate an inefficient signaller (Hobaiter & Byrne, 2011). Therefore, without ‘de-coding’ a species’ communication systems it is difficult to assess whether a sequence indicates greater complexity or inefficiency. My predictions relating to sequence-use assume they indicate greater complexity, but as this might not be the case, especially for gestural sequences, these are tentative predictions. I predicted that greater given and received tolerance would be associated with a higher rate of signalling overall, a higher rate of using goal-directed communication, greater persistence or elaboration, greater multimodal signal-use and potentially greater sequence-use, depending on the modalities used.

Methods

Study Sites and Subjects

The sample in the current study includes six of the ten chimpanzee and bonobo groups included in chapter 3 study; three captive chimpanzee groups (groups A and B from Leipzig Zoo, and Vallée des Singes group) and three bonobo groups (Leipzig Zoo group and groups A and B from Vallée des Singes). As in Chapter 3, I included only individuals independent of their mother, resulting in an N of 30 chimpanzees and 27 bonobos (see chapter 3 methods for detailed description of these groups and individuals).

Equipment

All focal and aggression data were recorded with a Panasonic HDC-SD90 camcorder, with a Sennheiser MKE 400 microphone attached. Grooming and scan data were recorded using an Olympus Digital Voice Recorder WS-853. Communication focal videos were coded using Noldus Observer XT 10 event logging software (http://www.noldus. com/animal-behavior-research).

Ethical Note

This study complied with the ASAB/ABS guidelines for the use of animals in research and was granted ethical approval by the Biology Ethics Committee, University of York. All data collection was approved by the zookeepers in charge of the apes.

Data Collection

Observational data on communication, grooming, aggression, reconciliation and feeding proximity were collected between April-August 2017 in Leipzig Zoo, Leipzig, Germany, and between July-Sep 2018 at Vallée des Singes, Romagne, France. The methods section in chapter 3 details the data collection procedures for grooming, aggression, reconciliation and feeding proximity. Focal animal sampling (Altmann, 1974) was used to collect communication data. Focal animals were chosen based on their visibility/audibility and to ensure a similar observation time across individuals and in the three primary behavioural contexts [mean, standard deviation and range of observation times in minutes: Rest = 25.19 (6.20), 16.22-44.47. Feed = 23.23 (5.09), 15.19-44.58. Groom = 23.12 (6.60), 5.51-42.50]. Once a focal animal was chosen, they were continuously audio and video-recorded for 15 minutes with the aim of capturing all facial, vocal and gestural signals produced by the individual. Any signals from other individuals within 5m that triggered, or were a response to, the focal animal’s signals were also recorded. Thus the camera was zoomed in as close as possible on the focal individual while capturing their whole body, and also attempting to include individuals within 5m unless it compromised the visibility of the focal. Vocalisations produced by the focal animal were commentated on, so even quiet vocalisations that were not caught by the microphone were recorded. I ensured a minimum of one hour total observation time per individual, which consisted mostly of feed, rest and groom contexts, with other behavioural contexts (e.g. travel) making up the remaining time.

Communication Coding

The software Observer XT 10 was used to code multiple aspects of communication produced by the focal subject in the focal communication videos, as well as continuous data on their behavioural context and availability of each communicative modality (facial, gestural, vocal). This allowed for extraction of accurate frequencies and rates of the communication measures for each individual as a function of the behavioural context and time available in each communicative modality.

Behavioural contexts.

The behavioural context of the focal subject was continuously coded. I excluded any behaviours or observation time that occurred during sleep (as no signals could occur), aggression (as aggression data were a priority and sufficient focus could not be given to signal-use), play (as many communication measures would have been biased towards those individuals who happened to display this rarer, highly communicative context during their observation time) or interacting with an infant or juvenile (as I excluded signals directed towards dependent individuals). This left five contexts for inclusion in communication analyses (feed, rest, groom, travel, other; see table 14 for definitions). Following Wilke et al., (2017), for each context to be coded, the behaviour had to continue for at least 20 s (an interruption of up to 5 s was allowed), after which interruptions of up to 15 s were allowed, provided the individual always returned to the original behaviour. Where behaviours occurred simultaneously, a hierarchy was used to determine behavioural context, with the more active behaviour given priority: feed>travel, groom>holding food, actively feeding>being groomed.

Table 14

Definitions for behavioural context of focal subject

Context	Definition
Rest	When the focal animal is sitting or lying down relatively still with eyes open, and for the majority of the time not feeding, grooming, or playing. Also includes time spent self-grooming (attending to their own body/fur – combing through the fur or picking at the skin to remove dirt or parasites). (Wilke et al. 2017)
Feed	When the focal animal is collecting and eating, or extracting moisture from, food (e.g. leaves, bark, fruit, honey), faeces, OR are an anticipation of feeding. They may move short distances in the process of doing this. If they resume feeding after a period of chewing, this continues to be counted as feeding. If they chew (not including licking fingers/hands) for more than three min without resuming collecting and eating more food after this, this is coded as resting after three min of chewing. If they have food in their hand, this can be considered feeding, but if they hold food without feeding for three minutes without resuming, this can be considered no longer feeding. If they are chewing on enrichment, this can be considered feeding, but not if they are just holding it in their hand or in their mouth.

Groom with other	When the focal animal is attending to the body/fur of another individual – combing through the fur or picking at the skin to remove dirt or parasites (Wilke et al., 2017)
Travel	When the focal animal is running, walking or standing for the majority of the time.
Other	Behaviour that cannot be considered rest, feed, groom, travel, sleep, play, aggression, or interacting with dependent individual (e.g.,. drinking water)

Modalities available.

The availability of all modalities (facial, gestural, vocal) was coded at all times to indicate which type of signals could be reliably coded if they were produced by the focal subject (see appendix 13 for coding definitions). This allowed for accurate calculation of signal production rates. Following Wilke et al. (2017), to be coded as available, the modality had to be available for at least 20 s (an interruption of up to 5 s was allowed during this time), after which interruptions of up to 15 s were allowed, as long as the original modality then became available again. As an exception, if a modality was mostly unavailable but briefly became available and the focal produced a signal from that modality, the modality was coded as available for this brief period and the signal was also coded (e.g., the individual's face cannot be seen, she turns around for 2 s, produces a facial expression and turns away again).

Signal Types

Each signal produced by the focal individual was coded and categorised according to the respective vocal, gestural and facial expression repertoires reported in the literature for chimpanzees and bonobos (Chimpanzees; vocalisations [Slocombe & Zuberbühler, 2010], gestures [Hobaiter & Byrne, 2011], facial expressions [Parr, Waller, Vick & Bard, 2007]. Bonobos; vocalisations [de Waal, 1988], gestures [Graham, Furuichi & Byrne, 2017], facial expressions [de Waal, 1988]. See appendix 14 for descriptions).

Signal Bouts.

All signals produced by the focal subject, whether vocalisations, gestures or facial expressions, that occurred within 30 seconds of each other and were directed to the same audience were coded as part of the same signal bout. The audience could be specific (directed towards a specific individual, indicated by the body unambiguously orienting towards that individual) or non-specific (the body directed towards a group of individuals, or not towards anyone in particular). Signals directed towards a new audience (i.e, directed to a specific individual, or from a specific to a non-specific audience) were coded as a new signal bout. All signal bouts were coded according the modalities of the component signals (e.g., a bout with vocalisations and gestures was coded as a Vocal-Gestural bout). Each signal bout was also coded as being an initiation or a response (i.e., whether the first signal in the bout was feasibly triggered by another individual's signal that occurred within 10 seconds before the onset of the focal signalling bout); and whether there were any other individuals within 5m when it was produced.

Goal-Oriented Communication

Some instances of communication were categorised as "goal-oriented communication episodes". These are episodes that Hobaiter & Byrne (2011) termed "intentional communication", and described it as "communication deliberately targeted to a particular recipient, with the aim of influencing their behaviour in a specific way". Following their criteria, signals accompanied by one or more of the following were considered goal-oriented:

> Audience checking: The signaller shows signs of being aware of the potential recipients and their state of attention, e.g. turning to look at the recipient before signaling.
>
> Response waiting: The signaller pauses at the end of the communication and maintains some visual contact.
>
> Persistence: The production of further signals, after response waiting and in the absence of a response that in other cases is taken as satisfactory (In certain circumstances, such persistence might be impossible, for example where an adult carries an infant away; these cases are marked as unable to persist, rather than no persistence.)

Communication was only coded as goal-oriented if it contained a signal previously found to have a meaning associated with an immediate goal; therefore, gestures (Graham, Furuichi & Byrne, 2017; Hobaiter & Byrne, 2014) and pant-grunts (Bygott, 1979; Clay, under review; Goodall, 1986; de Waal, 1981). However all signals directed to the same individual in that time were considered part of the same episode, until the receiver produced an apparently satisfactory outcome (ASO) which determined the end of the goal-oriented episode. An ASO is "any outcome that resulted in the cessation of communication and that represented a plausible desire on the part of the signaller" (Hobaiter & Byrne, 2014). Where no ASO occurred, a goal-oriented episode was considered terminated if the focal directed a signal to a new audience, or if they ceased signalling for thirty seconds. As with signal bouts, goal-oriented episodes were coded as being an initiation or a response. Additionally, the identity of the communicative partner was coded, along with whether persistence or elaboration occurred (persistence is repeating the same signal or a component of a multi-component signal after >1sec, elaboration is producing a different signal after >1sec).

Multimodal Signals

When the focal subject produced signals from two or more modalities that overlapped temporally, the overlapping period was coded as a multimodal signal. All multimodal signals were categorised based on the modalities of the component signals (e.g., a facial expression produced at the same time as a vocalisation was coded as a Facial-Vocal Multimodal Signal).

Sequences

When the focal subject produced more than one different signal type within 1 second of one another, but with no temporal overlap, this was coded as a sequence. As with multi-modal signal, all sequences were categorised based on the modalities of the component signals.

Inter-coder Reliability

To test the reliability of the video coding performed by EK, two independent researchers second-coded a proportion of the videos following the same coding scheme. One researcher coded 16.50% of the chimpanzee focal videos (N=14 videos), obtaining a mean Cohen’s kappa value of 0.92, and a different researcher coded 23.81% of the bonobos focal videos (N=10 videos), obtaining a mean Cohen’s kappa value of 0.80. Both kappa values indicate excellent levels of coder agreement (Fleiss, 1981). To obtain these values, the Reliability Analysis function in Observer XT 10.5 was used which allows comparison of two different event logs for one video.

Measures

Dominance Style

To measure dominance style, I used the dominance style components from chapter 3, which comprise the following behavioural measures (see chapter 2 for measure definitions):

- *Chimpanzee dominance style component*:
  Aggression Directional Inconsistency Index (DII), Counteraggression, Rate of low intensity aggression and feeding proximity.

- *Bonobo component 2 (‘Relationship symmetry and value’*):
  Aggression DII, Counteraggression and Reconciliation
- *Bonobo component 3 (‘Conflict style’):*
  Rate of low intensity aggression and aggression intensity.

In order to measure ‘given tolerance’ (how tolerant an individual is of lower-ranking partners) and ‘received tolerance’ (how tolerant higher-ranking partners are to an individual) for individuals, as in chapter 2, I calculated given and received tolerance versions of the dominance style components. To do this, for each individual I first formed two versions of the behavioural measures comprising the component scores; a given tolerance and a received tolerance version (see table 15), and then computed Z scores for each measure, standardising across all individuals in the species. Aggression intensity was reversed-scored to make it consistent with other measures, i.e., so that a higher value indicates greater tolerance. I could not calculate a given or received version of feeding proximity as this would have relied on identifying whether a higher or lower ranking partner was within 1m during scans which could not be extracted from the data. Next, for each individual I calculated a given and received version of the species dominance style component scores from the average of the Z scores of all measures comprising the component, excluding feeding proximity. For example, an individual chimpanzee’s given tolerance component score would be formed from the mean of the Z scores of given tolerance versions of aggression DII, counteraggression and rate of low intensity aggression.

Table 15

Definitions of given and received tolerance versions of behavioural measures comprising dominance style components for an individual

	Given Tolerance Version	Received Tolerance Version
Aggression DII	The mean aggression DII score with all lower ranking partners (aggression DII = proportion of aggressive bouts within a dyad in which the roles of aggressor and victim occurred in the least frequent direction)	The mean aggression DII score with all higher ranking partners (aggression DII = proportion of aggressive bouts within a dyad in which the roles of aggressor and victim occurred in the least frequent direction)

Counteraggression	The percentage of aggressive bouts that an individual initiated (in the role of aggressor) against a lower ranking individual, in which the victim retaliated	The percentage of aggressive bouts in which an individual retaliated against a higher-ranking aggressor.
Rate low intensity aggression	Per hour, the number of aggressive bouts without physical contact that the individual initiated (in role of aggressor) against a lower ranking partner	Per hour, the number of aggressive bouts without physical contact that the individual was the initial victim to a higher-ranking aggressor.
Aggression Intensity	The percentage of aggressive bouts that they initiated (in role of aggressor) against a lower-ranking victim, in which they used physical contact	The percentage of bouts where they were the initial victim to a higher-ranking aggressor, in which the aggressor used physical contact
Reconciliation	The mean conciliatory contact tendency score between the individual and all lower-ranking partner	The mean conciliatory contact tendency score between the individual and all higher-ranking partner

Note: DII refers to directional inconsistency index. See chapter 3 methods for explanation of how conciliatory contact tendency score was calculated.

Communication

Table 16 outlines all communication measures. Only communication which was initiated by the focal was included, in order to exclude cases of contagious communication such as pant-hoot chorusing (Ghiglieri 1984) and to include only communication that showed a motivation on the part of the focal to communicate rather than just reacting. A signal produced by the focal was considered a response and not an initiation if it was feasibly triggered by another individual producing a signal within 30 seconds before (e.g., joining in a pant-hoot chorus. Partner raises arm and focal raises his/hers to join hands). I excluded any instances of communication that were clearly directed at a zookeeper. A minimum criterion of two signal bouts per individual was required for inclusion in the multimodal signal-use and sequence-use measures, two goal-oriented episodes where first signal got no response for inclusion in the persistence/elaboration measure.

Rates were calculated using observation times of each modality; e.g., vocal rate was calculated by dividing the number of bouts with a vocalisation by the observation time (in hours) that vocalisations were available. For signal bout rate, I summed the rates of each bout type (facial only, gestural only, vocal only, facial-gestural, facial-vocal, vocal-gestural and facial-vocal-gestural bouts), which were calculated using observation times of any modality that occurred in the bout type; e.g., rate of facial-vocal bouts was calculated by dividing the number of facial-vocal bouts by the observation time (in hours) that either face or vocalisations were available.

Table 16

Description of all measures of communication

Measure	Description
Signal Bout Rate	The number of signal bouts produced by the individual per hour that were initiations and not responses.
Vocal Rate	The number of signal bouts initiated by the individual per hour that contained a vocalisation
Gesture Rate	The number of signal bouts initiated by the individual per hour that contained a gesture
Facial Rate	The number of signal bouts initiated by the individual per hour that contained a facial expression
Multimodal Signal-Use	The proportion of signal bouts (initiations only) produced by the individual that contained a multimodal signal
Sequence-Use	The proportion of signal bouts (initiations only) produced by the individual that contained a sequence
Episode Rate	The number of goal-oriented episodes produced by the individual per hour, that were initiations.
Persistence/Elaboration	The proportion of (initiated) goal-oriented episodes where the first signal received no response, and the individual persisted with the same, or a different signal following >1sec pause

Data Analysis

To provide an overview of the communicative strategies across modalities in both species, I provided a descriptive summary of communication measures, and of the use of vocal, gestural and facial modalities in signal bouts, multimodal signals and sequences. I also compared the rates of multimodal signals across behaviour contexts, and response rates to unimodal compared to multimodal signals. Where possible, I compared my results to that of previous literature.

To test whether individuals’ communication is related to the tolerance they give to lower-ranking partners, or the tolerance they receive from higher-ranking partners, I conducted linear mixed models (LMMs) and generalised linear mixed models (GLMMs) in *R* using the lme4 package (Bates, Maechler & Bolker, 2015). I examined chimpanzees and bonobos separately, with each model including one of their given or received tolerance component scores as the fixed effect, group as a random effect and one of the six communication measures as the outcome variable. Table 17 summarises these models. I only included a random intercept because there was no a priori reason to expect variation in slopes for the fixed effects across groups, and because this would result in underpowered models. Sample size also did not permit a statistical test of the relationships between any bonobo dominance style component with ‘Persistence or elaboration’, so I examined these descriptively only in appendix 15.

Additionally, to test whether given tolerance Aggression DII predicts vocal rate across our captive sample in chimpanzees and bonobos, as found in Chapter 2 in a wild sample across twenty-six species, I constructed an LMM with given tolerance Aggression DII as the fixed effect, Species and Group as random effects, and vocal rate as the outcome variable (vocal rate is the number of signal bouts containing a vocalisation produced per hour).

I selected the most appropriate distribution for all models by inspecting diagnostic plots of the model residuals and residuals against predicted values. Where I could not identify a suitable distribution I report the results based on a Gaussian distribution and demonstrate that these results are similar across alternative distributions in appendix 16. I estimated parameters using restricted maximum likelihood in all LMMs, and using Laplace approximation in all GLMMs. In all GLMMs, the residual degrees of freedom were not significantly different from the combined residuals, indicating that there was no issue of overdispersion. To obtain p-values, I conducted likelihood ratio tests of each full model with the dominance style component as a fixed effect against a model without the effect.

Table 17

Summary of twenty-six models with a dominance style component score as the fixed effect, group as a random effect and a communication measure as the outcome variable.

Model		**Outcome variable**	**Random Effect**	**Fixed Effect**
a)	i)	Signal bout rate	Group	Chimpanzee Given Tolerance Component Score
	ii)	MM signal-use		
	iii)	Sequence-use		
	iv)	Episode rate		
	v)	Persistence/Elaboration		
b)	i)	Signal bout rate	Group	Chimpanzee Received Tolerance Component Score
	ii)	MM signal-use		
	iii)	Sequence-use		
	iv)	Episode rate		
	v)	Persistence/Elaboration		
c)	i)	Signal bout rate	Group	Bonobo Given Tolerance Component 2 Score (Relationship symmetry and value)
	ii)	MM signal-use		
	iii)	Sequence-use		
	iv)	Episode rate		
d)	i)	Signal bout rate	Group	Bonobo Given Tolerance Component 3 Score (Conflict Style)
	ii)	MM signal-use		
	iii)	Sequence-use		
	iv)	Episode rate		
e)	i)	Signal bout rate	Group	Bonobo Received Tolerance Component 2 Score (Relationship symmetry and value)
	ii)	MM signal-use		
	iii)	Sequence-use		
	iv)	Episode rate		
f)	i)	Signal bout rate	Group	Bonobo Received Tolerance Component 3 Score (Conflict Style)
	ii)	MM signal-use		
	iii)	Sequence-use		
	iv)	Episode rate		

Results

Summary of Communication Use

Overview of Communication Measures

Table 18 provides a summary of communication measures. Descriptively, this shows that chimpanzees on average signalled more frequently than bonobos, which appears to be due to more frequent production of gestural and facial signals. While chimpanzees produced a higher proportion of multimodal signals than bonobos, there was considerable variation within species. On average, less than ten percent of the communication of both species was multimodal, as found by Wilke et al., (2017) and Hobaiter et al., (2017) in wild chimpanzee samples. Bouts including gestures were the most common in both species, mirroring findings by Wilke et al., (2017) and Pollick and de Waal (2007).

Table 18

Summary of communication measures across chimpanzees and bonobos

Communication Measure	**Chimpanzees**		**Bonobos 27**	
Signal bout rate (N per hour)	N=30	7.82 (4.62) /hr	N=27	4.94 (2.63) /hr
Vocal bout rate (N per hour)	N=30	2.01 (2.36) /hr	N=27	2.03 (2.51) /hr
Gesture bout rate (N per hour)	N=30	5.36 (3.71) /hr	N=27	3.16 (2.39) /hr
Facial bout rate (N per hour)	N=30	2.16 (2.98) /hr	N=27	0.46 (0.76) /hr
Multimodal signal-use (% bouts)	N=29	7.21 (13.38) %	N=25	5.37 (13.75) %
Sequence-use (% bouts)	N=29	10.54 (12.81) %	N=25	6.59 (9.91) %
Episode rate (N per hour)	N=30	5.57 (4.36) /hr	N=27	2.94 (2.28) /hr
Persistence/Elaboration (% episodes without initial response)	N=19	32.61 (25.87) %	N=7	34.45 (20.90) %

Note: Values refer to mean value per individual (standard deviation in brackets).

Use of Communicative Modalities

I examined the use of the three modalities (vocalisation, gestures and facial expressions) in signal bouts, multimodal signals and sequences in our sample.

Table 19 provides a breakdown of signal bouts by modality across chimpanzees and bonobos. This shows that the majority of signal bouts of both species included a gesture, as found by in Pollick & de Waal (2007). Of the three modalities, the use of facial expressions differed the most between the two species, with chimpanzees on average producing more than twice the proportion of facial expressions as bonobos. In both species, the majority of signal bouts contained signals from just one modality. However, descriptively, chimpanzees combined signals from different modalities in the same bout more often than bonobos, as found by Pollick & de Waal (2007).

I separately examined the proportion of bouts in which subjects combined vocalisations with signals from other modalities, to provide a closer comparison to Taglialatela et al. (2015). I found that 59.70% of chimpanzees' 67 vocal bouts and 29.03% of bonobos' 62 vocal bouts also contained signals from other modalities. This shows that while the majority of signal bouts produced by both species contained signals from just one modality, the majority of chimpanzee vocalisations were produced in close proximity to a gesture or facial expression, comparable to the 50% found by Taglialatela et al., (2015) in captive chimpanzees.

Table 19

Summary of use of communicative modalities across signal bouts in chimpanzees and bonobos

	Chimpanzees	**Bonobos**
% Bouts with Vocalisations	26.55 (23.05) %	29.65 (35.88) %
% Bouts with Gestures	70.86 (24.43) %	71.20 (31.10) %
% Bouts with Facial Expressions	23.16 (26.45) %	11.94 (21.86) %
% Bouts with signals from more than one modality	16.90 (17.87) %	12.03 (23.44) %

Note: values represent mean and standard deviation of all individual in each species. A signal bout could include signals from different modalities, so the total percentage of bouts across the three modalities is greater than 100%.

Figure 14 shows the breakdown of the different modalities used in multimodal signals in our sample as well as the wild chimpanzees from Wilke et al., (2007; excluding the ‘fixed’ multimodal signals they included, such as a pant-hoot paired with a pant-hoot face). This shows that vocal-gestural multimodal signals were the most common across all samples. However, the captive chimpanzees used in this sample used a higher proportion of facial expressions in their multimodal signals compared to bonobos or wild chimpanzees.

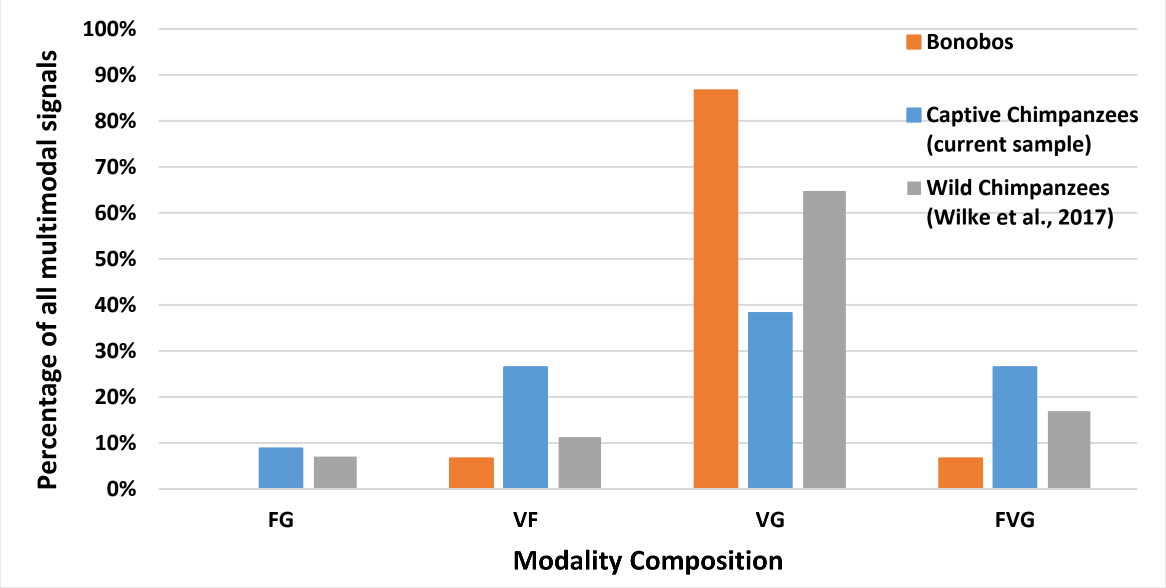


Figure 14 – Modality breakdown of multimodal signals produced by bonobos (N multimodal signals = 15), captive chimpanzees in our sample (N multimodal signals = 34) and wild chimpanzees from Wilke et al., (2007; N multimodal signals = 71, in rest, feed, groom, travel only).
FG = facial-gestural. VF = vocal-facial. VG = vocal-gestural. FVG = facial-vocal-gestural

Figure 15 shows the breakdown of the use of modalities within sequences in our sample. This shows that sequences containing gestures only were the most common in both species. Indeed, 78.13% of chimpanzees’ sequences and 81.82% of bonobos’ sequences contained a gesture, and no sequence consisted only of vocalisations or only of facial expressions.

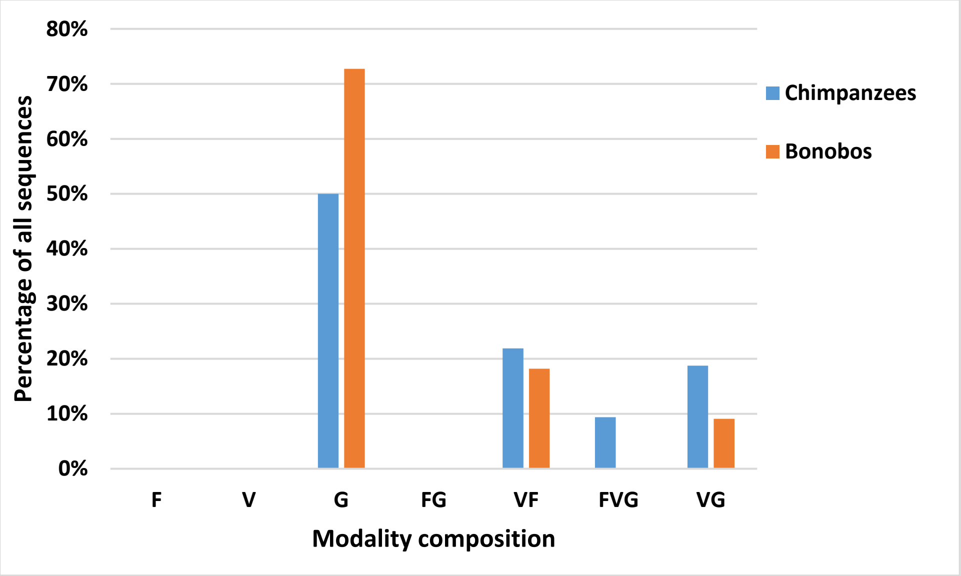


Figure 15 - Modality breakdown of sequences produced by chimpanzees (N sequences = 32) and bonobos (N sequences = 11) in our sample. F = facial. V = vocal. G = gestural. FG = facial-gestural. VF = vocal-facial. VG = vocal-gestural. FVG = facial-vocal-gestural

Multimodal Signal Rates across contexts

I examined the rate of multimodal signal production across the three main behavioural contexts; rest, feed and groom. As demonstrated by figure 16, on average both species produced the most multimodal signals in the feeding context, followed by groom and then rest. However, chimpanzees produced multimodal signals at a more even rate across the three contexts compared to bonobos. My results contrast with Wilke et al., (2017) which found that wild chimpanzees produced multimodal signals at the lowest rate during feeding context compared to in groom or rest.

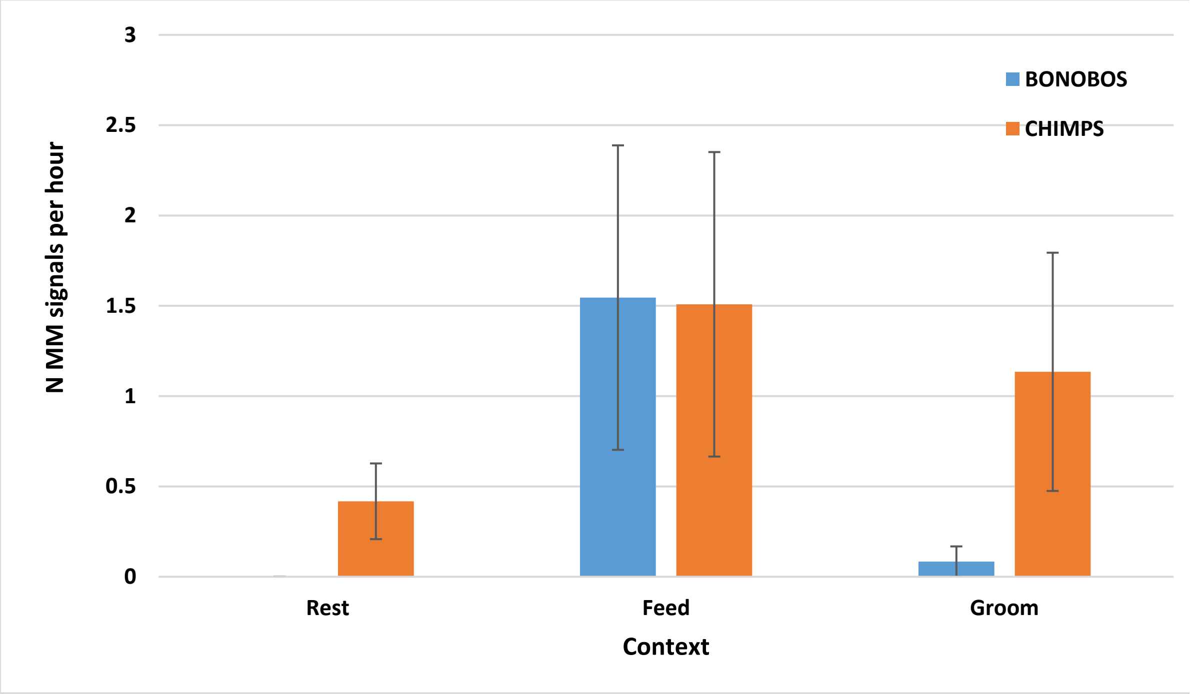


Figure 16 - Production rate of multimodal signals across three main behaviour contexts in chimpanzees and bonobos in our sample.

Figure 17 displays the breakdown of different modalities used in multimodal signals across the three main contexts of rest, feed and groom, in our sample as well as the wild chimpanzees from Wilke et al., (2017).

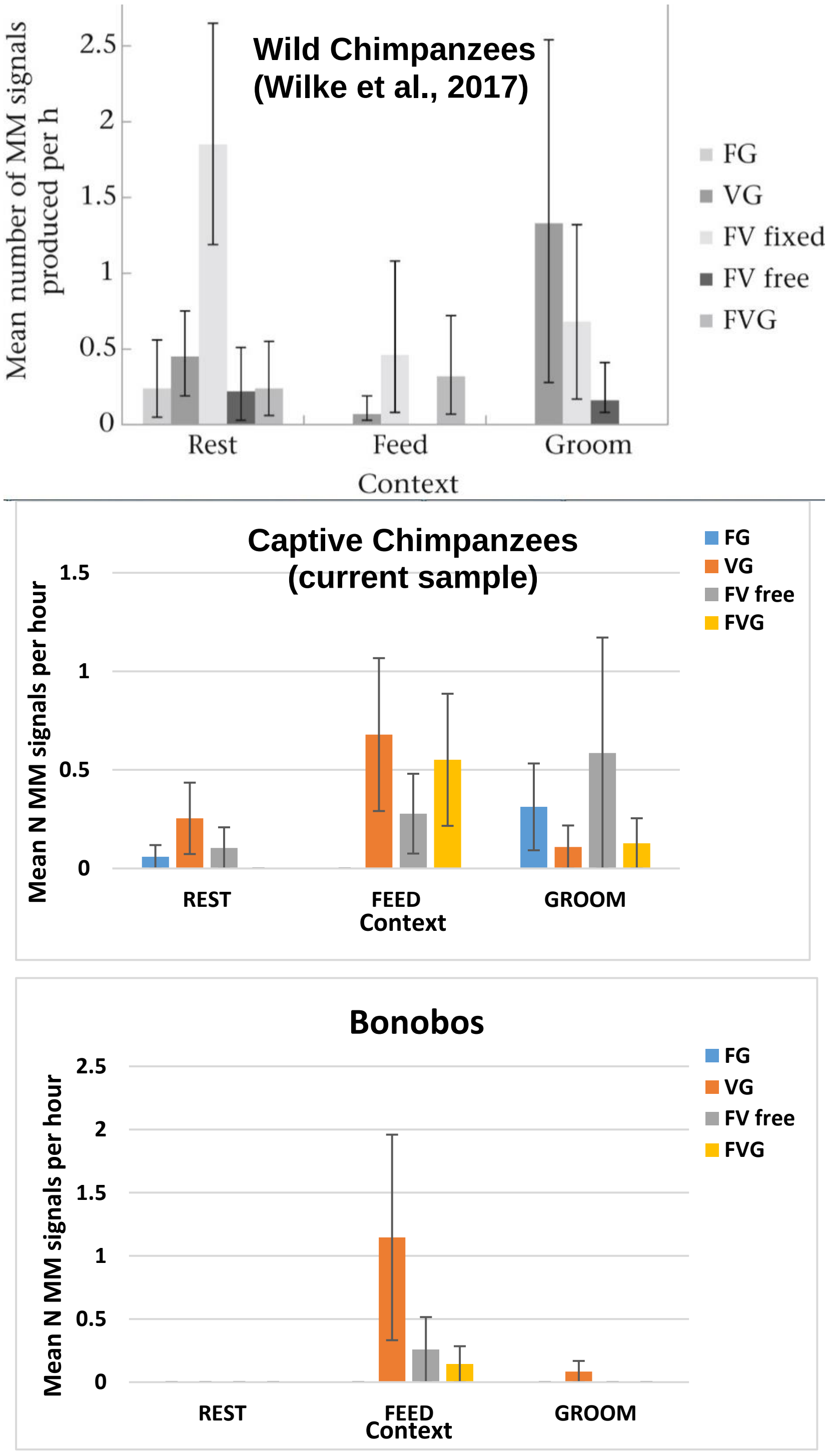


Figure 17 – Rate of multimodal signals, broken down by modalities used, across rest, feed and groom. The top panel is directly from Wilke et al., (2017) and contains fixed multimodal signals not included in the current sample. Error bars represent standard error. FG = facial-gestural, VG = vocal-gestural, FV = facial-vocal, FVG = facial-vocal-gestural. UM vs MM response rates

I compare the response rate to UM and MM signals within communicative episodes in table 20. In both species, if the first signal in an episode was MM, it received a response a smaller percentage of the time than if it was UM. Although this pattern is based on a small number of episodes started with a MM signal, it does contrast to Pollick & de Waal's (2007) finding that recipients are more responsive to MM signals (by their different definition) compared to UM gestures, and Wilke et al's (2017) finding that gestural-vocal MM signals are more likely to elicit a response than UM vocal signals alone.

Table 20

Response rate towards unimodal (UM) compared to multimodal (MM) signals within episodes

	Percentage of episodes that received a response if:	
	First signal was MM	**First signal was UM**
Chimpanzees	35.29%	41.78%
Bonobos	33.33%	65.56%

Note: Chimpanzees produced 163 episodes, of which 17 had a MM signal as the first signal, and 146 with a UM signal as the first signal. Bonobos produced 96 episodes, of which 6 had a MM signal as the first signal, and 90 with a UM as the first signal.

Dominance Style and Communication

Chimpanzees

My models indicated that among chimpanzees, given tolerance was not related to any communication measure, but greater received tolerance was related to a higher signal bout rate, episode rate and use of multimodal signals (see figure 18). Table 21 shows result statistics for all models. These results indicate that while being tolerant of lower ranking partners appears to have no relation to communication, chimpanzees who received more tolerance from higher-ranking partners produced signal bouts and goal-oriented communication episodes at a higher rate, and produced a higher proportion of multimodal signals.

Table 21

Summary of likelihood ratio tests comparing models with a communication measure as the outcome variable, group as random effect, and a dominance style component as the fixed effect, to a model without a fixed effect.

Outcome variable	**Model Statistics**	**Fixed Effect** **a) Chimpanzee Given Tolerance Component Score**	**b) Chimpanzee Received Tolerance Component Score**	**c) Bonobo Given Tolerance Component 2 Score**	**d) Bonobo Given Tolerance Component 3 Score**	**e) Bonobo Received Tolerance Component 2 Score**	**f) Bonobo Received Tolerance Component 2 Score**
i) Signal bout rate	N	27	26	19	23	16	24
	X^2	0.505	12.707	6.811	0.092	0.104	0.018
	p	0.477	<.001***	0.009**	0.762	0.747	0.892
ii) MM signal-use	N	26	25	17	21	15	22
	X^2	0.668[3]	5.938	0.218[3]	0.005[3]	1.006[3]	1.466[3]
	p	0.414[3]	0.015*	0.640[3]	0.942[3]	0.316[3]	0.226
iii) Sequence-use	N	26	25	17	21	15	22
	X^2	0.493[1]	<.001	5.302	5.849[2]	0.247	1.229[3]
	p	0.483[1]	0.976	0.021*	0.016*[2]	0.619	0.268
iv) Episode rate	N	27	26	19	23	16	24
	X^2	0.730[1]	9.500[1]	0.467[1]	0.687	0.122	1.004[1]
	p	0.393[1]	0.002**[1]	0.494[1]	0.407	0.727	0.316[1]
v) Persistence/ Elaboration	N	17	16	NA	NA	NA	NA
	X^2	0.343	1.072				
	p	0.558	0.300				

Note: Results are based on linear mixed models (ie., using a Gaussian distribution) unless otherwise indicated. Significant results highlighted in yellow. *$p<.05$, **$p<.01$, ***$p<.001$

[1] Gaussian distribution with log10 transformation on the dependent variable

[2] Generalised linear mixed model using a gamma distribution with an inverse link.

[3] No ideal distribution could be identified. Results based on model using Gaussian distribution, but results of models using alternative distributions are shown in appendix 16.

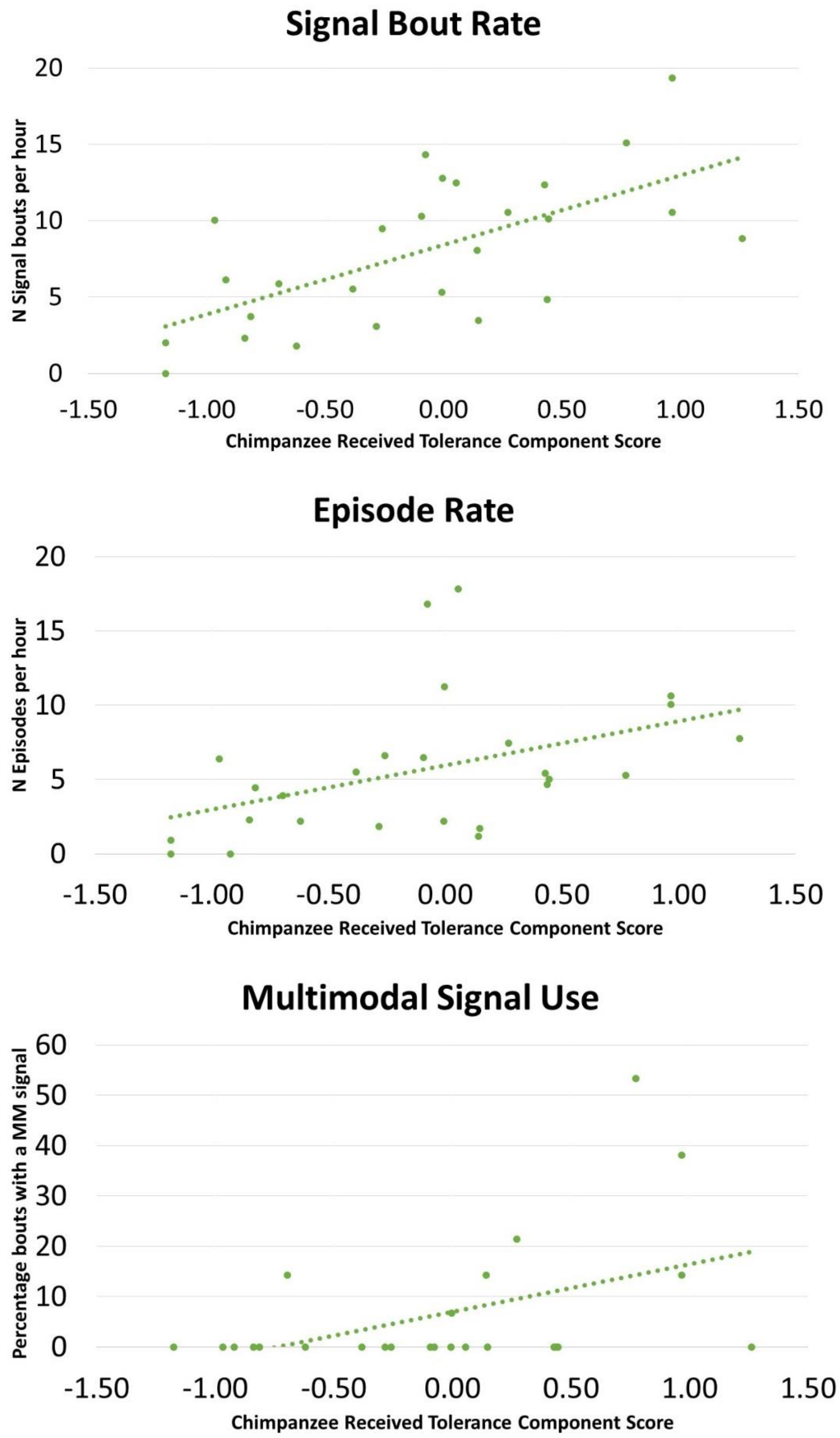


Figure 18 Relationship between Chimpanzee Received Tolerance Component Score and three communication measures (all significant at p<.05); signal bout rate, rate of goal-oriented communicative episodes, and proportion of bouts with a multimodal signal.

Bonobos

In contrast to the models including chimpanzees, the models including bonobos indicated that received tolerance was not related to any communication measure (with either component), but given tolerance was related to signal bout rate and use of sequences. Greater given tolerance as indicated by bonobo component 2 (relationship symmetry and value) was related to a higher signal bout rate and a lower use of sequences. This means that bonobos who reconciled more with, and had more symmetrical aggression with lower ranking partners, produced signals at a higher rate but used a lower proportion of signal sequences. I also found that greater given tolerance as indicated by bonobo component 3 (conflict style) was related to a higher use of sequences (see figure 19). This means that bonobos who used more frequent but less intense aggression towards lower ranking partners produced a higher proportion of signal sequences.

Overall, my results indicate that given tolerance is related to aspects of communication in bonobos, while received tolerance is related to aspects of communication in chimpanzees.

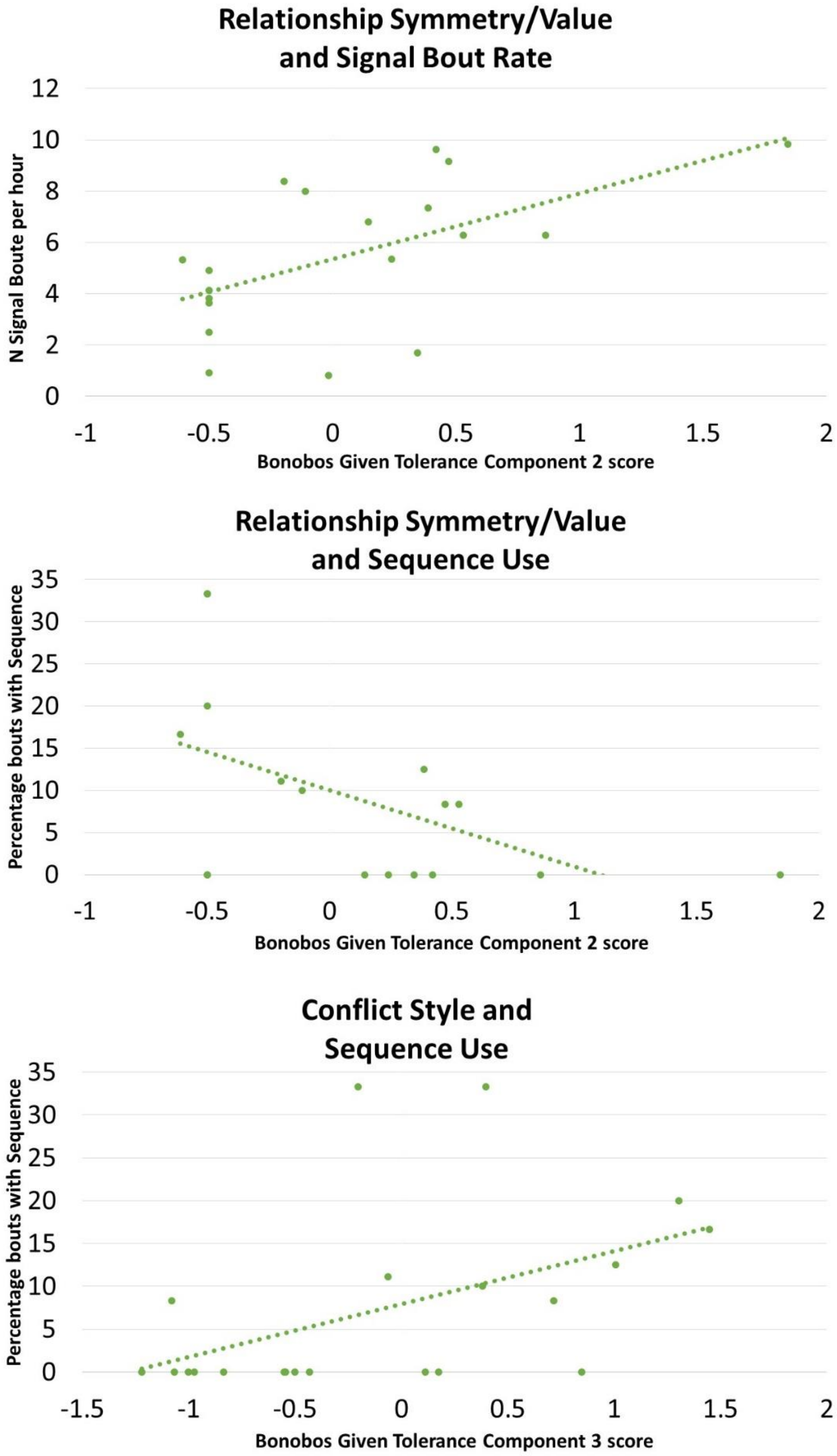


Figure 19 - Relationships between Bonobo Given Tolerance Component Score 2 (representing Relationship Symmetry and Value) and signal bout rate and sequence use, and between Bonobo Given Tolerance Component Score 2 (representing conflict style) and sequence use. These relationships are significant at p<.05.

Vocal Rate and Aggression DII

I tested whether one of our key findings from Chapter 2 (that given tolerance Aggression DII predicts a higher vocal rate in wild individuals from twenty-six species) replicates in the current captive sample of *Pan*. In an LMM using a log10 transformation on vocal rate, I found a trend towards significance (N=43, x^2= 3.374, p=0.066), suggesting that similar to the finding in wild primates, captive individuals whose aggression is more symmetrical with lower-ranking partners may vocalise at a higher rate (see figure 20). This finding provides evidence that the positive relationship between given tolerance aggression symmetry and vocal rate is relatively robust.

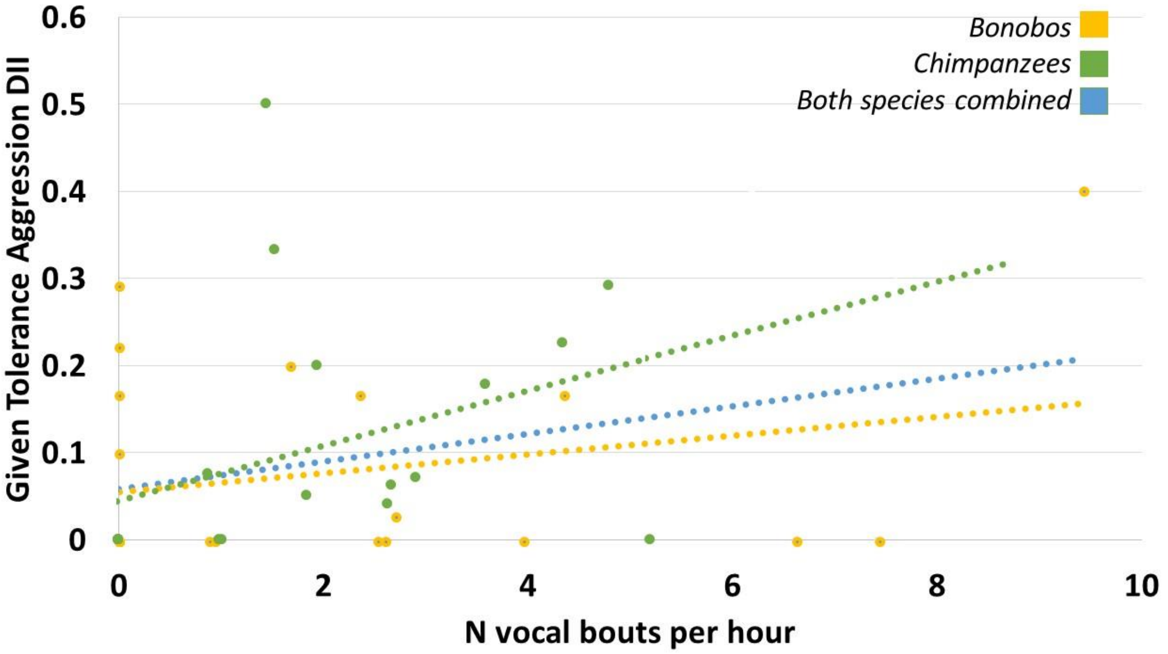


Figure 20 - Relationship between given tolerance Aggression DII and vocal rate across our captive sample of chimpanzees and bonobos

Discussion

The goal of this study was to provide an overview of chimpanzee and bonobo communication using a multimodal approach, and to test the relationship between dominance style and communicative strategies in individuals. I found interesting similarities and differences between chimpanzee and bonobo communication. Overall, on average, chimpanzees used more frequent and elaborate communication compared to bonobos, including a greater use of multimodal signals. However, multimodal signals were produced at a much lower rate compared to unimodal signals in both species, and both species also produced gestures at the highest rate, followed by vocalisations and then facial expressions. Regarding the relationship between dominance style and communication, I found evidence that received tolerance was related to aspects of communication in chimpanzees, while given tolerance was related to aspects of communication in bonobos. Specifically, I found that chimpanzees who received more tolerance from higher-ranking partners produced a higher rate of signals, more goal-oriented communication, and a higher proportion of multi-modal signals. I found that bonobos who were more tolerant towards lower-ranking partners in terms of relationship symmetry and value (ie., more aggression symmetry, counteraggression and reconciliation) produced a higher rate of signals and a lower proportion of sequences, while those who were more tolerant in terms of conflict style (ie., more frequent but less intense aggression) produced a higher proportion of sequences. These findings suggest that dominance style is an important predictor of communicative strategies, and that the nature of the relationship varies across species. Additionally, I tested whether greater aggression symmetry with lower-ranking partners (indicating tolerance) predicted a higher vocal rate in this sample, as found across a wide range of primate species in chapter 2, and found a positive trend towards significance. This provides evidence that this finding is relatively robust.

I have provided a comprehensive description of many aspects of captive chimpanzee and bonobo communication using a multimodal approach. Generally, I found similarities in the use of communicative modalities in our captive chimpanzee sample compared to that of wild chimpanzees. The use of multimodal signals was generally low in both species in our sample; as found by Wilke et al., (2017) and Hobaiter et al., (2017) in wild chimpanzees, unimodal signals were produced more than ten times as often as multimodal signals. This is in contrast to the higher rates of multimodal communication reported by Pollick and de Waal (2007) and Taglialatela et al., (2015) in captive chimpanzees, which is likely due to their differing definitions for multimodal signals which allowed temporal gaps of up to 10 and 2 seconds, respectively. As I also found a higher incidence of multimodal sequences and signal bouts than multimodal signals in this sample, it is likely that it is more common for chimpanzees and bonobos to combine signals from different modalities in close proximity compared to combining them with temporal overlap. I found that in both chimpanzees and bonobos, gestures were the most commonly produced modality, as found by Wilke et al., (2017) and Pollick & de Waal (2007). However, overall I found that the chimpanzees in our sample displayed more frequent and elaborate communication compared to the bonobos. They produced a higher rate of signalling and of goal-oriented communication, and a greater use of sequences and multimodal signals. The higher rate of signalling appears to be related to higher rates of gestures and facial expressions compared to bonobos, as their vocal rates were more similar. Chimpanzees tended to combine signals from different modalities more than the bonobos; they had a higher rate and proportion of multimodal signals, and a higher proportion of signal bouts and sequences with signals from multiple modalities. This is consistent with Pollick and de Waal's (2007) findings that chimpanzees produced vocal/facial signals alongside gestural signals more often than bonobos. However, as their study suffered with issues of pseudo-replication, and my study provided only a descriptive overview, future research should statistically test differences in the frequency and complexity of chimpanzee and bonobo communication, preferably in wild and captive samples.

Dominance style appears to be related to communication in both species, though in bonobos tolerance relates to the higher-ranking partner's communication, while in chimpanzees it relates to that of the lower-ranking partner. My findings in bonobos mirrors the findings from chapter 2, suggesting that it is more likely that tolerance increases pressure on dominant individuals' communicative strategies, rather than alleviating constraints on those of subordinates. I found that the opposite appears to be true in chimpanzees. This could potentially be explained by the fact that intra-group killings are known to occur in chimpanzees, but not in bonobos (Gruber & Clay, 2016). The possibility of a fatality could make communication misunderstandings riskier for subordinate chimpanzees, meaning that their communication is more constrained by despotic dominant partners than that of subordinate bonobos. Future research should test the relationship between received tolerance and communication across species known to display lethal intra-group aggression. The fact that I did not find given tolerance to predict communicative strategies in chimpanzees was surprising. This could be related to captivity, as individuals may be less able to use force to achieve goals (e.g., keepers often throw food to individuals to ensure all receive some), making the need to use communication to achieve goals similar in tolerant and despotic dominant individuals. However, as conditions were similar in bonobos it is unclear why captivity would affect the relationship in chimpanzees but not bonobos. Given tolerance in terms of aggression symmetry does appear to predict a higher rate of vocalising in chimpanzees, so there could be some functional difference in the use of different modalities that relates vocal, but gestural or facial communication, to given tolerance. Future research should assess whether there are differences in the use of the different modalities in functions such as achieving goals or affiliating.

Examination of the specific communicative measures related to dominance style can provide insight into the reasons behind their linkage. My finding that chimpanzees' received tolerance predicted an increased use of goal-directed communication suggests that there may be more opportunity for subordinate partners to make requests through communication within tolerant compared to despotic relationships. However, the lack of a relationship between received tolerance and the use of persistence/elaboration within goal-directed episodes could indicate that persisting with an unresponsive partner is still risky or futile for a low-ranking individual, even with a tolerant partner with whom they can make initial requests. Interpretation of the relationship between received tolerance and multimodal signal-use depends on the function of multimodal signals in chimpanzees, which is currently uncertain (Wilke et al., 2017). Such signals have the potential to transmit more information than the unimodal components (Partan & Marler, 1999) and thus represent greater complexity (Freeberg et al., 2012). In this case, my finding would provide support for the social complexity hypothesis. However, multimodal signals can also serve redundant functions and increase the likelihood of successful transmission in a noisy environment (Partan & Marler, 1999). Indeed the finding that subjects produced more multimodal signals in the feeding context, unlike the wild chimpanzees in Wilke et al., (2017), supports this suggestion, as feeding events are acoustically noisy in captivity, meaning vocal signals may not be easily received by listeners. In this case, my finding would suggest that subordinate chimpanzees are more efficient or effective communicators when higher-ranking partners are tolerant.

My findings in bonobos may provide insight into the reasons for the link between given tolerance and communication. I found no evidence that given tolerance was related to the rate of goal-directed communication in either species, which does not support my assertion that dominant individuals who are more tolerant use communication to achieve goals in lieu of threat of force. However, the finding that bonobos' given tolerance predicted a higher rate of signalling overall suggests that tolerance may increase pressure on dominant partners to communicate, not necessarily to achieve goals, but potentially to nurture relationships to achieve or maintain rank. I found that bonobos' dominance style components ('relationship symmetry and value' and 'conflict style') predicted the use of sequences in opposite directions. This was unexpected and difficult to understand. The vast majority of bonobos' sequences contained gestures, which could suggest that greater sequence-use indicates reduced efficiency in communicating (Liebel et al., 2004). As such, the link between more symmetrical/valued relationships and lower sequence use suggests that more tolerant bonobos are more effective communicators. It is difficult to understand why more tolerant conflict style would be related to less efficient communication, though as argued in chapter 3, relationship value and symmetry may be a better indicator of dominance style in bonobos than conflict style.

Here I have provided a detailed description and comparison of vocal, gestural, facial and multimodal communication in multiple groups of chimpanzees and bonobos, and tested its relationship with dominance style. My findings suggest that while captive chimpanzees may communicate more frequently and elaborately compared to bonobos, their use of communicative modalities shows a similar pattern to bonobos as well as to their wild counterparts. Notably, the use of multimodal signals was low across all samples, though combining signals from multiple modalities in close temporal proximity may be more common. I have shown that the relationship between dominance style and communication varies strikingly across even closely related species, as communication appears to be more closely linked to dominance style for the dominant partner in bonobos, but for the subordinate partner in chimpanzees. My findings show that dominance style is an important predictor of communication across multiple modalities, though the relationship between these factors should be closely assessed within each species.

Chapter 4: General Discussion

Summary of findings

In this thesis I conducted three empirical studies with the aim of furthering our understanding of dominance style and how it relates to communication in primates. In the first study (chapter 2) I examined dominance style and vocal communication in a broad sample of species across the primate order; probably the largest dataset of its kind to date. I found that individuals who had greater aggression symmetry with lower-ranking partners (indicating greater tolerance) vocalised at a higher rate than those with more unidirectional aggression, and that more despotic species had larger repertoires of vocalisations related to the management or reinforcement of the hierarchy. This indicates a linkage between dominance style and vocal communication at both the individual and phylogenetic level. In the second study (chapter 3) I took a closer look at the dominance style construct in two species; chimpanzees and bonobos. Here I found that the dominance style framework initially proposed for macaques maps more readily onto chimpanzees than bonobos, as behavioural measures appear to represent a single construct in chimpanzees, but are represented by two separate constructs in bonobos (‘relationship symmetry and value’ and ‘conflict style’). I also found that there were no clear differences in any of the dominance style measures in chimpanzees and bonobos, but that there was considerable variation within species; across groups, sexes, living conditions, and, in chimpanzees, sub-species. This challenges the traditional narrative than bonobos are universally the more tolerant *Pan* species, and highlights impressive behavioural flexibility within each species. In the third and final empirical study (chapter 4) I was able to test the relationship between dominance style with a wider range of communication measures than chapter 2, using a multimodal approach in captive chimpanzees and bonobos. I found that in bonobos, the tolerance an individual gives to lower-ranking partners predicted communication, while in chimpanzees, the tolerance an individual receives from higher-ranking partners predicted communication. This highlights that the relationship between dominance style and communication may differ across species. A more detailed description and interpretation of the findings are provided in the empirical chapters, but here I focus primarily on these key findings. I will begin by discussing what these findings tell us about the dominance style construct and its measurement across primates, and go on to address what they tell us about the reasons between its linkage with communication. I will then discuss how and why our findings relate to the social complexity hypothesis, and explore the likelihood that dominance style is stable across generations which is highly relevant for understanding its potential effect on evolved communication systems. Finally I will summarise suggestions for future directions that would be valuable in furthering our understanding of dominance style and its relation to communication in primates.

What is dominance style? Measuring dominance style across species

My findings in chimpanzees provide evidence that the macaque dominance style framework applies outside of the macaque genus to some extent. Thierry (2000; 2007) describes a ‘behavioural suite’ in macaques, with a number of behavioural variables co-varying across macaque species. The term dominance style (A.K.A. social style; Flack & de Waal, 2004; Thierry et al., 2008; Zhang & Watanabe, 2014) describes the overarching construct of these co-varying measures. These measures could therefore be used to quantify dominance style in macaques, but Thierry (2000) cautioned about their use outside of the macaque genus. The co-variation of these measures (and therefore the application of this framework) outside macaques has since been largely unexplored. In chapter 3, five previously used behavioural measures of dominance style co-varied across individual chimpanzees, demonstrating that the ‘behavioural suite’ found in macaques is also found in chimpanzees. While this indicates that the construct of dominance style therefore appears to be similar in chimpanzees and macaques, there are some differences in that it may not be appropriate to place chimpanzees into dominance style ‘grades’ due to considerable intra-species variation. While there is evidence of some intra-specific variation in macaque dominance style (Zhang et al., 2014), Thierry et al. (2008) found that the largest difference between nine macaque species was more than seven times the largest difference between groups within species. In contrast, I found large differences in dominance style between chimpanzee groups, making categorisation of the species as a whole difficult. However, as I found Western chimpanzees to be more tolerant than other sub-species (and this could potentially explain the group differences), it may be appropriate to place different sub-species into grades although further research is needed to confirm this.

Some of my findings suggest that the macaque ‘behavioural suite’ is not universal across primate species. In chapter 2, I found that different behavioural measures of dominance style in macaques predicted communication variables differently in a sample of twenty-six primate species. This indicates that these behaviours may not measure the same construct, as one would otherwise expect them to predict communication similarly. In chapter 3, I found that two underlying components of dominance (‘relationship symmetry and value’, and ‘conflict style’) were unrelated in bonobos. This suggests that different behavioural measures of dominance style in macaques and chimpanzees may be measuring different constructs in bonobos (e.g., aggression rate and counteraggression measure different constructs in bonobos, but both measure dominance style in macaques and chimpanzees). In other words, these two components are not part of a coherent dominance style construct as they are in macaques and chimpanzees. These findings support Thierry's (2000) suggestion that macaque dominance style measures cannot be assumed to co-vary in other species. It could be that there are smaller behavioural suites that do co-vary across a wider range of primate species (e.g., 'relationship symmetry and value' or 'conflict style'), but this requires further empirical testing in other species. Future research should conduct principle component analyses within species including a range of behavioural measures, to test which measures, if any, appear as behavioural suites in these species. In any case, my findings raise the question as to which behaviour or behavioural suite 'truly' measures dominance style.

I offer the suggestion that aggression symmetry may be the clearest indication of dominance style with the greatest likelihood of being widely applicable across primate species. A reminder that dominance style can be defined as 'the degree to which expressed behaviour corresponds with the direction of asymmetry within a dyad' (de Waal, 1989; de Waal & Luttrell, 1989). Hence, symmetry is fundamental to dominance style, as it represents deviation from expected asymmetry in behaviour. Measures of dominance style in macaques can loosely be summarised as measures of partner value, conflict management and symmetry. Partner value and the need to manage conflict provide the underlying rationale for why expressed behaviour would deviate from what might be expected based on dominance asymmetry, as discussed in chapter 1. But the final 'product' of these two features in a relationship is symmetry. Measures of partner value and conflict management would thus be expected to co-vary with this symmetry as they represent its underlying cause, but they may not directly measure dominance style. Additionally, the behaviours determining partner value and conflict management may vary across species. For instance, reconciliation indicates partner value (Cords & Thurnheer, 1993), and while some species may reconcile after conflicts via physical contact, another species could potentially reconcile in other ways (e.g., communication, food sharing). So, there may be difficulty in identifying a consistent measure of reconciliation across species. Symmetry within a relationship could also be indicated by different behaviours (e.g., affiliation), but aggression seems the most widely applicable across species. Dominance hierarchies are formed and maintained through aggression in the majority of primate species (Bernstein, 1976), althoughsome species may form and maintain hierarchies through non-aggressive means, with some humans being a prime example (Boehm, 1999). For this minority of species, aggression symmetry is unlikely to be a useful indication of dominance style. Although under some definitions, aggression asymmetry is necessary to indicate the existence of a dominance hierarchy (Lewis, 2002), I think there is value in identifying power asymmetries in non-aggressive species, and therefore identifying the extent of asymmetry (i.e., dominance style). Future research should seek to identify whether there is a behaviour that is common across species as an indication of power asymmetry, but until then, aggression asymmetry is likely the most widely applicable measure of dominance style across primates.

Some of my findings may provide preliminary support for the suggestion that aggression symmetry is the best measure of dominance style of those included in this thesis. One method of validating whether a variable measures a construct is to test whether it predicts other variables in the expected direction (i.e., predictive validity; Kelly, 1927). I presented several reasons why dominance style is expected to predict communication in chapters 1 and 2. Out of several tests of related predictions in chapters 2 and 4 (i.e., that tolerance predicts more frequent and elaborate communication, and despotism predicts richer repertoires of hierarchy-related signals), using different communication measures and species, only measures or behavioural indices that included aggression symmetry predicted communication in the expected direction. I only tentatively suggest that this provides predictive validity for aggression symmetry as a measure of dominance style due to the fact that these predictions represent empirical questions in this thesis. As such, future research should test whether aggression symmetry predicts other variables such as brain size to provide stronger predictive validity as a measure of dominance style.

Dominance Style and Communication

The findings in this thesis support the hypothesis that tolerance is linked to more frequent and elaborate communication, but the underlying reasons for this linkage are not entirely clear and may differ across species. Findings from the wide range of species in chapter 2 and those related to bonobos in chapter 3 suggest that tolerance places pressure on dominant individuals to communicate, while findings related to chimpanzees in chapter 3 suggest tolerance alleviates constraints on communication in subordinate individuals. As discussed in chapter 3, these differences may be related to species-specific factors such as intra-species lethal aggression. Across all of these findings, tolerance predicted the rate of communicating (vocal rate in chapter 2, vocal rate and overall signal bout rate in chapter 4). This points to tolerance being linked to a greater tendency to communicate, and therefore indicates that communication is more important within tolerant relationships. However, the simple rate of communication cannot tell us what is being communicated. Without “de-coding" a species' communication system, we cannot determine whether this increased rate is due to individuals communicating to make requests or to affiliate, for instance. As such, it is difficult to ascertain whether tolerance increases the need or opportunity to use communication to achieve goals, or to strengthen bonds in order to achieve or maintain rank, as I suggested in chapter 1. I initially expected that tolerance would increase the need for dominant individuals to communicate to achieve goals in lieu of threat of force, but findings in chapter 4 suggests that instead, tolerance may provide subordinate individuals the opportunity to use communication to achieve goals. It is possible however that these findings are specific to chimpanzees and bonobos and may not relate to the linkage between given tolerance and vocal rate in chapter 2. It seems likely that the reasons for this linkage may vary across species, considering the differences in findings between chimpanzees and bonobos in chapter 4. Future research should test the relationship between tolerance and specific communication types with a known function, such as affiliation, or goal-achievement as done in chapter 4, in a wide range of species. This could provide a more generalizable explanation for the linkage between tolerance and communication in primates. As discussed in chapter 4, some of my findings hint at the possibility that tolerance increases the efficiency or effectiveness of message transmission. It may be that the increased rate of communicating provides the practice necessary to improve this efficiency/effectiveness, though this remains an empirical question.

The findings in this thesis provide limited evidence in support of Freeberg et al.'s (2012) social complexity hypothesis. According to this hypothesis, a more tolerant dominance style should predict greater communicative complexity due its higher level of social complexity. Across individual level analyses the most consistent finding was that greater tolerance predicted a higher rate of communicating, but this does not necessarily indicate more complex signalling. In chapter 4, received tolerance predicted a greater use of multimodal signalling in chimpanzees. As discussed in Chapter 1, multimodal signal-use could be an indication of greater complexity, although carefully designed experiments or a very large sample of responses to multimodal and unimodal component signals would be necessary to assess this (Parco, Lartan & Owens, 2009; Wilke et al., 2017). Again, 'de-coding' a species' communication system is necessary for understanding the full extent of its complexity. Despite a clear link between tolerance and a greater tendency to communicate, our species-level analyses in chapter 2 provided no evidence that more tolerant species had more complex communication systems in terms of having larger vocal repertoires, or repertoires of social vocalisations. The findings in chapter 4 suggest that the relationship between dominance style and communication may vary across species. As such, the relationship between dominance style and repertoire size may be modified by unknown species-specific social or ecological variables. A major challenge in testing the social complexity hypothesis is that there are many dimensions of both social and communicative complexity (Fischer et al., 2017). As such, at this point I can only conclude that in contrast to Freeberg et al.’s (2012) hypothesis, the greater social complexity associated with tolerance does not appear to result in greater communicative complexity in terms of larger vocal repertoires.

The finding that tolerance appears to predict individual variation in communication but not in repertoire size could be due to a number of possibilities. Firstly, if tolerance exerts pressure on a species communication system, one would expect communication to provide individual fitness benefits within tolerant relationships. Some potential benefits could include improving or maintaining rank, increased access to resources, or improved social networks. It would be valuable to test whether communication provides such benefits for tolerant but not despotic individuals. Secondly, there may a time lag between the development of tolerance in a species and the complexity of the system. A species may use a simpler system more frequently or elaborately until a more complex system evolves. A valuable line of inquiry for understanding the evolution of communicative complexity would be to examine the interaction between the usage and complexity of communication systems in a large sample size of species. Some phylogenetic methods facilitate detection of evolutionary lag in discrete or continuous variables (Burt, 1989; Deaner & Nunn, 1999; Pagel, 1994) These would permit tracing the trajectories of these two aspects of communication in the primate lineage; to test whether changes in usage precede changes in complexity. If this is the case, the more tolerant species in our studies may have only become tolerant relatively recently in their evolutionary past, which would explain why they communicate more frequently or elaborately, but without greater complexity in their evolved system. Finally, tolerance should be relatively stable across evolutionary time in order for it to act as a selection pressure on a species communication system. I explore this issue in detail next.

Stability of Dominance Style

As touched on in chapter 2, dominance style may predict individual variation in communication, but if it is not consistent over generations, it cannot predict variation in a species communication system. It is therefore important to examine whether dominance style is inherited or learned, as this has implications for its potential to be stable within a species. Some degree of intraspecific variation in dominance style has been found in Japanese macaques (Zhang & Watanabe, 2014) and in the captive chimpanzees and bonobos in chapter 3. Dominance style does appear to be subject to learning to an extent.

For instance, in an experiment where rhesus macaques were housed with stumptails (a more egalitarian species), conciliatory tendency increased threefold in the rhesus macaques compared to their species-typical counterparts (de Waal & Johanowicz, 1993). This is evidence of a developmental aspect of dominance style, but genetic predisposition appears to have a considerable influence. Conciliatory tendency in the rhesus macaques in de Waal & Johanowicz's (1993) study was still significantly lower than that of the stumptails. Unsurprisingly, there is considerable interspecific variation in dominance style (Thierry, 2007). Thierry et al., (2008) looked at conciliatory tendency and counteraggression in 15 captive groups of nine macaque species and found that the largest difference between species was more than seven times the largest difference between groups within species. Thierry (2007) also describes a natural experiment wherein rhesus macaques were hand-reared and then reared among peers in the absence of an older generation to form a breeding group. This multigenerational troop today displays species-typical despotism, indicating that the experience of previous generations is not needed for this social style to emerge. In chapter 3, our findings suggest that sub-species could explain group differences in chimpanzee dominance style, which would point towards an inherited nature. These indicate that, while learning may play some role in dominance style, genetic inheritance may have a more robust effect. It may be the case that experience reinforces underlying predispositions. However it is not yet clear whether these findings and interpretations related to the learned vs. inherited nature of dominance style can generalise to other species.

There are multiple potential mechanisms by which dominance style traits are linked, whether learned or inherited, which has further implications for its potential to be stable across generations. Thierry (2007) argued that traits may be linked through two main mechanisms; originating from a common source, or from interactions between constituent parts of a system. He provides an example of gene pleiotropy as a common source mechanism; A single gene allele is related to impairment of serotonin efficiency (Canli & Lesch, 2007), and low serotonin is related to a behavioural suite including unrestrained aggression in rhesus macaques (Higley, Suomi, & Chaffin, 2011). Proximity of genes for different traits on a chromosome may also underlie their linkage as they have a low likelihood of being separated following recombination (Thierry, 2013). As well as at the genomic level, constraints at the level of the individual or social phenotype may underlie the coupling of traits, (Thierry, 2007; Thierry, Singh, & Kaumanns, 2004). Despotic macaque species are more reactive to the environment than egalitarian species; they become stressed more easily, are quicker to react aggressively and are less explorative (Clarke & Boinski, 1995; Thierry, Anderson, Demaria, Desportes, & Petit, 1994). Such differences in temperament may underlie links between multiple behavioural traits (Thierry, 2013). At the level of social phenotype, high intensity aggression, for instance, is not compatible with a high rate of counter-aggression as this combination would reduce survival ability (Thierry, 2013). Each of these described constraints at different levels are proposed as potential mechanisms for trait linkages.

Thierry (2013) argued that linkages and incompatibilities between traits act as constraints on the mutability of individual traits, so selection must instead act on the behavioural suite. This amounts to what he terms ‘correlational selection’. Strong interconnections between dominance style traits may stabilise their selection, allowing for their endurance over long time periods. Where changes do occur the entire suite of behaviour may change together. Thierry et al. (2004) suggested that this could occur through strong selection pressure on ‘pacemaker characters’; central traits that have knock-on effects on the rest of the traits. A computer modelling approach indicated that aggression intensity may be a central trait with regards to dominance style, as varying this trait only may lead to a switch from egalitarianism to despotism (Hemelrijk, 1999). Correlational selection appears to be a plausible mechanism by which dominance style is stable over evolutionary time. Our finding in chapter 3 that many dominance style traits co-vary in chimpanzees as they do in the distantly related macaques provides evidence that the behavioural suites may have endured and shifted together as suggested by Thierry (2013). However, our finding that co-variation is less clear in the closely related bonobos could suggest either that traits are interconnected in macaques and chimpanzees at the level of the social phenotype, or that bonobos are more derived than chimpanzees in this aspect of social behaviour. This could be resolved by investigating co-variation of dominance style traits in a range of primate species.

Correlational selection and the inheritance of dominance style traits provide the possibility that dominance style could be stable across generations and thus act as a selection pressure on communication systems, at least in some species. Despotism may be more likely to be stable than tolerance as indicated by some game theory models (Matsumara, 1999; Matsumara & Kobayashi, 1998). This could explain why we found no evidence in chapter 2 that tolerance predicted more complex vocal systems, but did find that despotism predicted a richer repertoire of hierarchy-related signals. However, Dobson (2012) found that tolerance predicted larger repertoires of facial expressions in macaques, indicating that tolerance may be stable in some macaque species. Indeed, studies focusing on phylogeny indicate that despite large ecological and climactic shifts, macaque social behaviour has changed relatively little over millions of years (Balasubramaniam et al., 2012; Thierry, Iwaniuk, & Pellis, 2000). It is highly plausible that stability in dominance style varies from species to species. A crucial next step is to identify species with a stable dominance style and test whether tolerance predicts variation in communication systems in these species. Empirical tests of the stability of dominance style within primate relationship throughout individuals’ lifetimes, and from generation to generation within a single group would indicate the likelihood that dominance style could endure over evolutionary time in the species. Examination of the stability of ecological conditions in a species could also provide additional evidence of stability of dominance style. The utility of socioecological models which predict that ecological variables explain dominance style has been brought into question due to a lack of empirical support for their predictions (Thierry, 2008; Clutton-Brock & Janson, 2012). However advocates of the models have argued that they have not been adequately tested and that adequate measures of ecological conditions have been difficult to obtain (Clutton-Brock & Janson, 2012; Koenig & Borries, 2009). We found preliminary evidence in chapter 3 that chimpanzees and bonobo differed in dominance style between wild and captivity. The possibility remains that ecological conditions could influence dominance style, so it would be valuable to first measure whether ecological conditions predict dominance style in a single species and then to examine whether such conditions were likely to be consistent over evolutionary time.

Future Directions

The findings of this thesis pave the way for future examinations of the construct of dominance style and how it relates to communication in primates. Firstly, although it was outside of the scope of this thesis, I believe that the co-variation of dominance style measures should be empirically tested within species across the primate order, using similar principle components analyses as in chapter 3 with chimpanzees and bonobos. This will shed light on the generalisability of the macaque dominance style framework across primates and the mechanisms through which different dominance styles emerges, and could identify which measures are the most comparable across species for quantifying dominance style. Secondly, the stability of dominance style should be assessed in each species by comparing measures within the same relationship or group at different time points spanning as long a time as is feasible. This would help to identify which species were likely to have displayed consistent dominance style over evolutionary time, which could in turn have exerted selection pressure on their communication systems. Thirdly, research which ‘decodes’ primate communication should continue in order to identify the meaning of primate signals and assess which aspects can be considered more complex than others. Although this is a particularly arduous task, it would provide insight into the reasons why dominance style and communication are linked and allow for more comprehensive tests of Freeberg et al.’s (2012) social complexity hypothesis. Fourthly, the individual fitness benefits of communicating should be assessed within tolerant compared to despotic relationships. For example, future research could test whether social networks are larger for individuals who communicate more within tolerant relationships compared to those who communicate more within despotic relationships. This could suggest that tolerance drives the evolution of communicative complexity by providing more communicative individuals with the fitness benefits of larger social networks. A failure to find any fitness benefit for communicative individuals within tolerant relationships could explain why we did not find a link between tolerance and evolved communication systems. Finally, the relationship between the rate and complexity of individual primate communication, and the relationship between usage and complexity of communication systems should be assessed across the primate order. This would provide a solid basis for understanding the evolution of complexity in communication systems, and for tracing its evolutionary trajectory.

In order to achieve the objectives outlined above, as well as many other research objectives in primatology, more large-scale collaborative research projects are vital. Due to the time consuming nature of primate data collection and complications associated with accessing primate subjects, relationships between variables of interest and characterisations of species are often based on studies of single primate groups (Atschul et al., 2019). This is problematic, because as demonstrated in chapters 2 and 3, relationships between variables may differ across species, and groups may differ within a single species. A wide range of species in a sample is essential for addressing questions related to primate evolution. Increasingly, the importance of accounting for phylogenetic signal is being recognised (Balasubramaniam et al., 2012), which can only be measured by including a large sample of species (preferably thirty or more; Freckleton et al., 2002). Generally, the only feasible way to obtain such samples is through a collaborative effort in which primatologists from various fieldsites contribute comparable data, as done in chapters 2 and 3. This comes with considerable challenges, most notably in relation to ensuring consistency of data across fieldsites. Data collection protocols and the definitions used for measures (e.g. ‘bout’) vary widely, creating issues with consistency. Ideally, the objectives of the research paper would be set out before data collection, and a comparable data collection protocol would be agreed upon to ensure that data were comparable across sites. The open-science approach of pre-registering studies would be a particularly valuable endeavour in collaborative projects, as many of the particulars of the study could be planned out, communicated and agreed upon in advance. Often these approaches may not be feasible, where instead previously collected data can be collated (as done in chapters 2 and 3). Here it is valuable to request data in as raw a form as possible and with as much detail about the measures and data collection protocol as possible to identify where inconsistencies may lie. Most crucially, effective communication between collaborators is key, including putting agreements in place in cases where data may need to be excluded (which due to the difficult nature of ensuring consistency across datasets could occur at various stages of the process). Adding to my comments here, which may be more applicable to observational research, Atschul et al., (2019) reviewed the benefits and limitations of collaborative experimental research in primate cognition in the context of ‘Many Primates’; an ongoing collaborative project which aims to address questions in primate cognition across multiple species and fieldsites. More collaborations such as these are highly valuable in the field of primatology, despite their logistical difficulties.

Conclusion

In sum, in this thesis I have provided the most comprehensive examination of dominance style in non-macaque species, and of how dominance style relates to communication in primates, to date. I have highlighted the similarities and differences of the dominance style construct in chimpanzees and bonobos in comparison with each other as well as with macaques, and provided quantifiable indices of dominance style in these two species. This can be highly valuable for measurement and comparison of dominance style in other groups of *Pan*, and for testing how tolerance relates to variables such as communication, cooperation and brain size. My findings challenge the traditional narrative that bonobos are more tolerant than chimpanzees, and demonstrate impressive behavioural flexibility in both species but particularly chimpanzees. I have shown that dominance style predicts individual variation in vocal communication at the individual and phylogenetic level across the primate order. I have also shown that tolerance predicts more frequent and elaborate individual communicative strategies in *Pan,* though for chimpanzees this is seen in subordinate individuals, while in bonobos it is seen in dominant individuals. These findings suggest that dominance style is an important social variable for understanding variation in communication in primates, but specific effects may vary across species. As is often the case, this research has generated many avenues for future research questions that would be valuable to pursue. However, overall the findings in this thesis advance our understanding of primate social behaviour and how it may shape individual communicative strategies as well as evolved communication systems.

Appendices

Chapter 2

Appendix 1 – Fieldsite details

Table A

Description of fieldsites, data collection dates and ethics for all datasets included in sample.

Species	**Binomial Name**	**Fieldsite Location**	**Site Description**	**Data Collection Dates**	**Ethics details**
Assamese Macaques	*Macaca assamensis*	Phu Khieo Wildlife Sanctuary.	The Phu Khieo Wildlife Sanctuary in north-eastern Thailand (PKWS, 16°05–35’N & 101°20–55’E) is part of the more than 6500 km2 interconnected and well-protected Western Isaan forest complex. It sanctuary covers an area of >1600 km2, with elevations ranging from 300 to 1300m above sea level. The pristine forest is composed of dense, dry evergreen vegetation with patches of bamboo forest and harbours a diverse community of large mammals and predators.	Jan 2016- Jun 2017	Research permission granted by the Department of National Parks, Wildlife and Plant Conservation (DNP) and the National Research Council of Thailand (NRCT); permit number 0002/470
Barbary Macaques	*Macaca sylvanus*	Middle Atlas mountains, Morocco	Middle Atlas Mountains, Morocco (33°24′N–005°12′W), at 1400-1950m above sea level. Temperate forest dominated by cedar and oak trees. Daily rainfall ranged between 0 and 117 mm (mean ± SE=3.96±0.28 mm/d). Air temperature ranged between –5.0 and 40.4 °C (mean ± SE=15.95±0.13 °C per day) and relative humidity between 0 and 100 % (mean ± SE=57.53±0.38 % per day)	Oct 2009- Apr 2011	Research permission given by the Haut Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification (Morocco)

Black Howler Monkeys	*Alouatta pigra*	Palenque National Park (Chiapas, Mexico)	The study groups live in Palenque National Park (17°27′51″ N, 99°01′30″ W). The park covers 1771 ha and includes 597 ha of primary tropical rain forest, 300 ha of regenerating forest, and 874 ha of pasture land.	Feb 2012- Jul 2012	The research accomplishes with the requirements of the Animal Care Committee of Universidad Nacional Autonoma de Mexico and adhered to the legal requirements of Mexico. Protocols were approved by the "Direccion General de Vida Silvestre (SEMARNAT), permit # GPA/DGVS/00692/08." This research adhered to the American Society of Primatologists principles for the ethical treatment of primates.
Bonnet Macaques	*Macaca radiata*	Bandipur National Park, Karnataka, India	Bandipur National Park (11.66°N, 76.63°E) in the southern state of Karnataka, India. Spanning over c. 874 km², with an elevation ranging from 680 m to 1,454 m ASL, this Park experiences a typical tropical climate, prevailing across the region. The Park falls within the Nilgiri Biosphere Reserve, at the junction of the Deccan Plateau and the Western Ghats, and is characterized mostly by dry deciduous forests, interspersed with moist deciduous forest patches and dry scrub. The annual rainfall cycle allows for the demarcation of a dry and a wet season, from December to May and June to November respectively. The average rainfall in the area falls in the range of 141.44 ± 19 mm during the period from June to September. Bandipur is host to a rich ensemble of flora and fauna, including diverse trees, insects, amphibians, reptiles, and birds, as well as small and large mammalian species. The most common primate species in this area is the bonnet macaque.	Feb 2013- July 2014	Research permission granted by the Forest Department, Government of India. The observational study protocol was approved by the ethics committee at the National Institute of Advanced Studies, Bangalore, India and the Manipal University, Manipal, India.
Bonobos	*Pan paniscus*	LuiKotale, Democratic Republic of Congo	Behavioural observations were collected on wild, habituated individuals from the Bompusa community of wild bonobos the LuiKotale field site, located near the	Nov 2013- Mar 2014	Research permit: Institut Congolais pour la Conservation de la Nature (MIN.0242/ICCN/DG/GMA/013/2013)

			Salonga National Park, DR Congo. Habituation began in 2002 and food provisioning has never been used. At the that time data were collected, the fully habituated community consisted of twelve parous females, two nulliparous females, six adult males, one sub-adult male and eighteen immatures. Age estimates were based on physical features, such as body size and dentition. Three immatures were considered independent of mother.		
Campbells Monkeys	*Cercopithecus campbelli*	Taï National Park, Ivory Coast	We observed and recorded two wild habituated groups of Campbell's monkeys in the Taï National Park, Ivory Coast (5°50'N, 7°21'W). The Tai National parc is a tropical evergreen lowland forest in the South-West part of Cote d'Ivoire. Vegetation is mainly composed of a dense ombrophilous forest with a continuous 40 to 60 meters canopy an emergent trees. Tropical rainy climate, with stable temperature range over the year (average: 24°C).	Feb 2006- July 2007	Research approved by the Ivorian Minister of Scientific Research and the Ivorian office of Parcs and Reserves (OIPR).
Chimpanzees	*Pan troglodytes schweinfurthii*	Kibale National Park, Uganda	The Kanyawara community of chimpanzees live in Kibale National Park in southwestern Uganda just north of the equator (0°13' to 0°41' N and 30°19' to 30°32' E). The study area is located in the north of the park and is made up of mostly moist medium-altitude evergreen forest with small areas of grassland, swamp, colonizing forest and pine plantation. The average elevation is 1500m above sea level and the daily temperature ranges from 14.9°C to 20.0°C. There are usually 2 rainy seasons (March-May and August-November) during the year with an annual average rainfall of 1,749mm.	Jun 2014- Mar 2015	Permissions to conduct this study were granted by the Ugandan Wildlife Authority and the Ugandan National Council of Science and Technology

Chimpanzees	*Pan troglodytes schweinfurthii*	Nyungwe National Park, Rwanda	The study was conducted in Nyungwe National Park (NNP), located in south-western Rwanda between 2°17′-2°50′S and 29°07′-29°26′E. NNP protects 1,019 km2 of Afromontane tropical forest (between 1,600 and 2,950 m ASL). The vegetation is a mosaic that includes open and closed forest, bamboo forest, swamp, moorland and open regions. NNP receives 1,744 mm of annual rainfall with an average maximum and minimum temperature of 19.6°C and 10.9°C, respectively. The region experiences a major wet season from February to May, a long dry season from June to August, with a minor wet season from September to November and shorter dry season from December to January.	Nov 2016- Dec 2017	Permissions to conduct this study were granted by the Rwandan Development Board and Rwandan Ministry of Education. Approval for our observational data collection protocols was given by the University of Western Australia's Animal Ethics Committee (F 18979). All research activities complied with the Rwandan government and national park authorities' regulations for the observation of chimpanzees.
Crested Macaques	*Macaca nigra*	Tangkoko Nature Reserve, Sulawesi, Indonesia	We studied two wild groups of crested macaques in the Tangkoko nature reserve (1°31′N 125°11′E), North Sulawesi, Indonesia (Macaca Nigra Project's field site, www.macaca-nigra.org). The reserve includes primary and secondary forest, regenerating abandoned gardens and scrubland. The reserve spans an altitude range of 0-1,351m and annual rainfall is 1,550-2,400mm.	Sep 2010- April 2011	The research complied with protocols approved by the Approval of project by the Animal Welfare and Ethical Review Body at the University of Portsmouth; adhered to the legal requirements of the United Kingdom and Indonesia; and adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.
Diana Monkeys	*Cercopithecus diana*	Taï National Park, Ivory Coast	We observed and recorded two wild habituated groups of Diana monkeys in the Taï National Park, Ivory Coast (5°50'N, 7°21'W). The Tai National park is a tropical evergreen lowland forest in the South-West part of Cote d'Ivoire. Vegetation is mainly composed of a dense ombrophilous forest with a continuous 40 to 60 meters canopy an emergent trees. Tropical rainy climate, with stable temperature	Feb 2009- June 2010	Research approved by the Ivorian Minister of Scientific Research and the Ivorian office of Parcs and Reserves (OIPR).

			range over the year (average: 24°C).		
Geladas	*Theropithecus gelada*	Simien Mountains National Park, Ethiopia	Data for this study come from three different bands in one community of wild geladas (~ 1,200 individuals) living in the Sankaber area of the Simien Mountains National Park in northern Ethiopia (13°15′N, 38°00′E, elevation: 3000-3300 m ASL) that has been monitored continuously since January 2006. This region is an Afroalpine grassland ecosystem, consisting of undulating grassland plateaus, scrublands, and Ericaceous forests. This region experiences a wet season from June to October and a dry season that runs from November to May. Annual rainfall is 1702 mm, and mean monthly temperature is 12.9°C (8.2-17.6°C) (Jarvey et al. 2018).	Jan 2009- Nov 2016 (a single year chosen per group; the one with the most data)	Research was approved by the University Committee on Use and Care of Animals at the University of Michigan and adhered to the laws and guidelines of Ethiopia.
Geoffreys Spider Monkeys	*Ateles geoffroyi*	Otoch Ma'ax yetel Kooj protected area (Yucatan peninsula, Mexico)	Otoch Ma'ax Yetel Kooh reserve, close to Punta Laguna village (Yucatan Peninsula, Mexico—20°38′ N, 87°38′ W). The habitat consists of a mosaic of vegetation that includes a 60-ha fragment of semievergreen medium forest (with trees up to 25 m height) and an area of forest in different stages of secondary succession (with trees less than 15 m height).	Sep 2016- April 2017	All protocols performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. Our study adhered to the legal requirements for field observations of animals in Mexico. Protocols were approved by the Direccion General de Vida Silvestre (SEMARNAT, permit #SGPA/DGVS/1405/15).

Geoffreys Spider Monkeys	*Ateles geoffroyi*	Runaway Creek Nature Reserve, Belize	Runaway Creek Nature Reserve is a 2,469-ha private reserve in central Belize, located 16km west of the Caribbean Sea coast. The reserve encompasses two main vegetative zones: pine savannah and semi-deciduous, broadleaf tropical forest, and is part of a larger area of approximately 58 km2 of continuous forest. At 20 - 120 meters above sea level, the terrain at Runaway Creek encompasses steep limestone karst hills, low valleys, and seasonal swamps. This area of Belize has a dry season from December - May and a wet season from June – November, in which it receives an estimated 2,000 - 2,200 mm of rain annually.	Jan-Dec 2009	All research protocols were approved and supported by the University of Calgary, Athabasca University, and the Natural Sciences and Engineering Research Council of Canada. Permission granted by the Belize Forestry Department, treasury receipt 1662659, Dr. Gil and Lillian Boese from the Foundation for Wildlife Conservation and the Zoological Society of Milwaukie.
Indris	*Indri indri*	Maromizaha Forest, Madagascar	Maromizaha New Protected Area (18°56'49"S, 48°27'53"E) is a mid-altitude (800 - 1200 m) tropical evergreen rainforest, with annual rainfalls of 1779 mm	Jun-Sep 2018	Data were collected with the approval of MEEF (Research Permit N° 91/18/MEEF/SG/DGF/DSAP/SCB.Re); our Department (Dept. of Life Sciences and Systems Biology, University of Torino, Italy) does not require ethical approval since our research does not imply animals handling or manipulation.
Japanese Macaques	*Macaca fuscata*	Yakushima, Japan	Study was conducted near the coast (0-400 m above sea level) on Yakushima Island (31N, 131E). The research site was covered with a warm temperate evergreen forest. Dominant tree species on the coastal forest are *Distylium racemosus, Ficus superba, Ficus microcarpa, Camelia japonica,* and *Ardisia sieboldii.* Temperature ranges from a minimum of about 3C to a maximum of about 32C, rainfall is between 100 and 400 mm each month but it is higher than 400 mm in June, which is the peak of the rainy season.	(1 group) Dec 2017- Jan 2018 (2 groups) Jun 2001- May2002	(1 group) Approval received from Primate Research Institute, Kyoto University (Japan). The research was conducted with permissions from Kagoshima Prefecture and the Yakushima World Heritage office (2 groups) Approval received from Liverpool John Moores University (UK) and Primate Research Institute, Kyoto University (Japan)

Kinda Baboons	*Papio kindae*	Kasanka National Park, Zambia	Directly from Petersdorf et al. (2019): “…habituated study population of the Kasanka Baboon Project in Kasanka National Park (KNP). KNP is located in the central province of Zambia and is bounded by the coordinates S12.40° and 12.66° latitude and E30.05° and E30.38° longitude (Willems, 2014). KNP is 450 km2 in area and is located 30 km east from the southwestern border of the Democratic Republic of Congo (The World Fact Book, 2014). The park lies within the belt of miombo-mopane woodland that stretches from Mozambique to Angola, with an altitude that varies from 1160 m to 1286 m above sea level and an annual rainfall of ~1100mm (KNP).”	Jun 2017- April 2018	IACUC (University Animal Welfare Committee at New York University) #17-1487; Department of National Parks and Wildlife, Zambia (research permit #DNPW/101/13/18)
Mongoose Lemurs	*Eulemur mongoz*	Ankatsabe forest, Madagascar	Boeny region of northwestern Madagascar, strong seasonal variation in precipitation (yearly average rainfall is 1700 mm) with a distinct rainy season during November to March. Seasonally dry broadleaf deciduous forest patches.	May-Jul 2017	Ankatsabe Forest - Research autorisation N°71/17/MEEF/SG/DGF/DSAP/SCB.Re delivered by the "Direction du système des aires protégées, Repoblikan'I Madagasikara"
Mountain Gorillas	*Gorilla beringei beringei*	Bwindi Impenetrable National Park, Uganda	We observed one group of mountain gorillas in Bwindi Impenetrable National Park (0°53–1°08N, 29°35–29°50E), Uganda. The study site consists of afromontane rainforest (altitude 1160–2600 m) which is characterized by steep hills and a dense understorey of herbaceous vegetation.	March 2007-Nov 2008	Resarch approved by Uganda Wildlife Authority and the Uganda National Council for Science and Technology
Olive Baboons	*Papio anubis*	Laikipia, Kenya	We studied two groups of wild baboons that range in Mukogodo region of Laikipia North on the Laikipia Plateau of central Kenya. These groups are part of a larger population that is monitored by the Uaso Ngiro Baboon Project (UNBP), directed by Dr Shirley C. Strum.	Jan-Dec 2014	The study conformed to U.S. and Kenyan laws and was approved by the National Commission for Science and Technology of Kenya and the Kenya Wildlife Service. The project was approved by the Arizona State University Institutional Care and Use Committee. All animal protocols followed the

			The baboons range in an area that is topographically diverse and averages 1718 m above sea level. The habitat is dry savanna and includes grassy plains, acacia woodlands and dry forests located on the banks of sandy riverbeds. Rainfall is typically concentrated during two wet seasons (March-June, November-December, but droughts are increasingly common. The baboons feed on a variety of grasses, herbs, sedges and the flowers, fruits and pods of a variety of shrubs and trees including several Acacia species. Recently, Opuntia stricta, a nonindigenous cactus, has invaded the area and has become an important part of the diet.		guidelines for the treatment of animals for teaching and research recommended by ASAB/ABS (2014).
Olive Baboons	*Papio anubis*	Gashaka Gumti National Park, Nigeria	Gashaka-Gumti National Park, in the north east of Nigeria. The Kwano research site, approximately 10 km into the forest from the border of the national park, is located at GPS coordinates, 07°degrees20minsN - 011degrees35minsE. Habitat is a mosaic of gallery and montane forest and guinea woodland savannah. The Kwano research station rests at approximately 400 m above local sea level. Average annual rainfall at Kwano was 2009 mm (2001 - 2002, 2004-2006). Total annual rainfall for the year 2007 (the first field season of study) was 1787mm; and for 2008 was 1727mm (the second field season). The mean maximum monthly temperature (between 2000 and 2008) was 32.5 degrees celsius. And the mean minimum monthly temperature for the same period was 21 degrees celsius. In December and January of both field seasons, the minimum temperature reached was 14 degrees celsius with a maximum temperature of 41	Feb 2007-May 2008	All research protocols followed were assessed and approved by Roehampton University's Research Degrees Board, which included ethical approval, and adhered to all legal requirements of both Nigeria and the UK. Research within Gashaka Gumti National Park was possible with permission by the Nigerian National Parks Service under a research permit issued to Volker Sommer.

			degrees celsius recorded in March 2008.		
Red fronted lemurs	*Eulemur rufifrons*	Kirindy Forest, Madagascar	Kirindy Forest/CNFEREF is a dry deciduous forest in western Madagascar, located at sea level 60 km northeast of Morondava	Mar-Aug 2011	All protocols were approved by the Malagasy Ministry of the Environment
Red-tailed monkeys	*Cercopithecus ascanius*	Kibale National Park, Uganda	The Ngogo research station (0° 29′ N and 30° 25′ E) consists primarily of old-growth rainforest with interspersed grasslands, regenerating forest, and gallery forest. The site is at an approximate altitude of 1,350 m but the terrain is moderately hilly. The area experiences two rainy and two dry seasons annually, and Ngogo experienced an average of 1,463mm of rainfall during the study period.	Jan 2012- Jun 2015	Permissions to conduct this study were granted by the Uganda Wildlife Authority, the Uganda National Council for Science and Technology and the Uganda Office of the President. Data collection protocols were approved by the Institutional Animal Care and Use Committee (IACUC) of the University of New Mexico (11-100661-MCC), and deemed exempt by the IACUC at the University of California, Santa Barbara. M.B. conducted all research activities in compliance with Ugandan national laws.
Ring Tailed Lemurs	*Lemur catta*	Beza Mahafaly Special Reserve, Madagascar	Data were collected at Beza Mahafaly Special Reserve, a protected reserve in the southwest of Madagascar (23°30’S lat., 44°40’E long.). This reserve contains two non-contiguous forests, riverine forest in the eastern area of the reserve (Parcel I, 80 ha) and dry forest in the western area (Parcel II, 500 ha). All data were collected from individually-known lemurs in the Parcel I forest.	Mar-July 2010	All data were collected in Madagascar with the approval of MNP. This research protocol was approved by the University of Toronto Animal Care Committee, and adhered to the legal requirements of Madagascar.
Sooty Mangabeys	*Cercocebus atys*	Taï National Park, Ivory Coast	This study was conducted in Taï National Park in South-western Ivory Coast (5°50’N, 7°21’ W). The park is the largest remaining major block of primary forest in West Africa and covers approximately 454,000 ha of continuous forest. With a mean annual temperature of 24°C, a mean annual rainfall of 1,875 mm (average of 2012–2015; data: Taï Monkey Project), and a distinct dry season in December–January, the	Jan 2014- Jul 2014	We used non-invasive methods for the observation of the subjects in their natural habitat. The animals were identified by physical features like scars, body size and shape, and they were all habituated to human observers. Research permission and ethical clearances were granted by the Ministère de la Recherche Scientifique et Technique de Côte d’Ivoire.

			forest is classified as 'tropical moist'.		
Verreaux's Sifaka	*Propithecus verreauxi*	Kirindy Forest, Madagascar	Kirindy Forest/CNFEREF is a dry deciduous forest in western Madagascar, located at seas level 60 km northeast of Morondava	Jan 2012- Apr 2013	All protocols were approved by the Malagasy Ministry of the Environment
Verreaux's Sifaka	*Propithecus verreauxi*	Bezà Mahafaly Special Reserve, Madagascar	Bezà Mahafaly Special Reserve is a community-based conservation area in southwest Madagascar (44.613 E, 23.662 S) that protects gallery, dry deciduous, and spiny forest. Annual rainfall is variable, but averages ~700mm during non-drought, non-cyclone years. The reserve was originally protected as two non-contiguous parcels in 1986 and then expanded in 2015 to include new core areas, sustainable use zones, and buffer zones.	Jun-Oct 2018	All protocols were approved by the Malagasy Ministry of the Environment
Vervet Monkeys	*Chlorocebus pygerythrus*	Soetdoring Nature Reserve, South Africa	The study was conducted at the Soetdoring Nature Reserve in the Free State Province, South Africa (28° 50′ S, 26° 2′ E). The average altitude at the site is 1450m and rainfall averages 400 – 600 mm per annum (Janecke 2002). Two biomes occur in the reserve, Grassland and Nama-Karoo, and the two dominant vegetation units are grassland and riparian vegetation (Janecke 2002). Rainfall is highly seasonal, with the summer months (November and March) being the wettest and hottest part of the year. January and February are the hottest months, with maximum and minimum temperatures averaging around 30°C and 15°C respectively. The cold, dry, season lasts from late May to early August, with minimum daily temperatures during the coldest period averaging -2°C and maximum temperatures around 18°C.	Jan-Dec 2012	The study was approved by New York University's University Animal Welfare Committee (Protocol number 12-1391) and was conducted with the permission of the Department of Economic Development, Tourism and Environmental Affairs of the Free State Province of South Africa (Permit number 01/9912).

Vervet Monkeys	*Chlorocebus pygerythrus*	Mawana Game Reserve, South Africa	The study took place at the Inkawu Vervet Project, located in the Mawana Game Reserve, a private farm of 12’000 hectares in KwaZulu-Natal, South Africa (S28°00.327; E031°12.348). According to the Köppen-Geiger climate classification (Kottek et al. 2006), KwaZulu-Natal enjoys a subtropical climate characterized by warm wet summer from November to February and mild moist to dry winter from May to August.	May 2014- Jan 2015	All animals have been fully habituated to the presence of human observers and did not show any signs of disturbance related to researchers. We used standard data collection methods for behavioural data and all data were collected in accordance with the ethical ASAB/ABS guidelines for the use of animals in research. Local permission was given by Ezemvelo KZN Wildlife, the governmental organisation in charge of Kwa-Zulu Natal wildlife conservation and biodiversity.
Western Gorillas	*Gorilla gorilla gorilla*	Mondika Research Center, Congo	Date were collected at the Mondika Research Center (02°21′859″N; 016°16′465″E), 50 km2 of tropical rainforest situated in the Djeke triangle bordering Nouabale-Ndoki and Dzanga-Ndoki Parks, on the border between Republic of Congo and Central African Republic. Altitude < 400 m; fruit production vary seasonally, with major fruiting season occurring between June and September. The forest is a mosaic of Gilbertiodendron dewevrei monodominant forest, mixed-species semi-evergreen forest and swamp forest. The site has never been logged.	May 2009- May 2010	Permits to conduct research at Mondika were obtained by the Ministry of Economy and Forest of Republic of Congo. The study and protocols were approved by Stony Brook University (IACUC)

White Faced Capuchins	*Cebus imitator*	Santa Rosa National Park, Costa Rica	Santa Rosa National Park (10°50'30"N, 85°37'0"W) was established in 1971 on former cattle grazing pastureland (Allen, 2001). It is now known as Sector Santa Rosa (SSR) and is part of the broader Área de Conservación Guanacaste (ACG). The ACG became an UNESCO world heritage site in 1999 and includes approximately 147,000 hectares of tropical ecosystems, including marine, dry forest, cloud forest, and rainforest. The ACG is made up of 18 separate sectors of which SSR was the first to be created. SSR is located in the northwestern corner of Costa Rica, 35 km north of the city of Liberia and 40 km south of the Costa Rican boarder with Nicaragua. SSR is made up of regenerating tropical dry forest and is punctuated by two drastically distinct seasons; the majority of rain falls in the wet season from mid-May to mid-December [mean = 1497 mm/year] and nearly no rainfall in the dry season from mid-December to mid-May dry season (Fedigan, 1993; Melin et al., 2014).	Feb 2013- Jul 2017	Data collection was approved by the Ministereo of Ambiente y Energia, Systema Nacional Del Areas de Conservacion, Del Area de Conservacion Guanacaste (Permit No. R-SINAC-ACG-PI-054) and the IACUC at Tulane University (Protocol #0399).

Yellow Baboons	*Papio cynocephalus*	Amboseli National Park, Kenya	From Alberts et al., 2005; “The Amboseli basin (2°40' S latitude, 1100 m altitude) is a semi-arid short-grass savannah ecosystem located in an ancient lake basin at the base of Mt Kilimanjaro in East Africa. Mean annual rainfall is 348 mm, but the range of annual rainfall is quite large, from less than 150 mm to more than 550 mm. In the pattern typically described for the area, rainfall occurs in two seasons centered in November-December (the "short rains") and in March-May (the "long rains"), with a “short dry season” in January and February and a “long dry season” during June through October. However, the only component of this pattern that does not vary from year to year is the long dry season. The short rains or the long rains, or both, may fail, or substantial rain may fall during the short dry season. This variability contrasts sharply with the predictability of the long dry season: between the end of May and the last few days of October, virtually no rain falls. Mean daily maximum and minimum temperatures exhibit small but predictable seasonal changes; diurnal changes are much larger in magnitude than those that occur seasonally.”	Jan-Dec 2016	The study conformed to U.S. and Kenyan laws and was approved by the National Commission for Science and Technology of Kenya and the Kenya Wildlife Service. The project was approved Institutional Care and Use Committees at Duke University, Princeton University, and the University of Notre Dame.

Appendix 2 – Sampling effort

Table A

Sampling effort across all groups included in the sample. Observation times provided for vocal rate, groom and aggression data as well as the number of individuals and/or dyads included in all individual and group level measures.

	Observation Times: Mean (SD) hours per individual for focal data, total N hours for all-occurrence data			**Individual Level Measures: N of Individuals included**									**Group Level Measures: N of individuals/Dyads included (Average of groups calculated per species)**						
				Received Tolerance Measures				**Given Tolerance Measures**				**Feeding Proximity**	**Aggression DII**		**Aggression Intensity**	**Counter-Aggression**	**Groom DII**		**Feeding Proximity**
Group	**Vocal Rate Data**	**Groom Data**	**Aggression Data**	**Aggression DII**	**Intensity**	**Counter-aggression**	**Groom DII**	**Aggression DII**	**Intensity**	**Counter-aggression**	**Groom DII**		**N dyads**	**N individuals**	**N individuals**	**N individuals**	**N dyads**	**N individuals**	**N individuals**
Assamese Macaques	2.11 (0.28)	65.32 (17.00)	65.32 (17.00)	15	16	16	13	16	16	16	14	A	59	17	18	18	52	18	A
Barbary Macaques (Group 1)	186.15 (60.00)	186.15 (63.25)	186.15 (63.25)	8	8	8	5	7	9	9	6	A	106	18	17	17	92	18	A
Barbary Macaques (Group 2)	55.92 (20.2)	55.93 (21.86)	55.93 (21.86)	5	3	3	2	6	5	5	6	A	75	16	NA	NA	55	16	A
Black Howler Monkeys (Group 1)	52.1 (1.13)	51.10 (1.24)	51.10 (1.24)	1	B	B	2	1	B	B	3	A	1	2	B	B	4	4	A
Black Howler Monkeys (Group 2)	64.37 (1.15)	64.38 (1.30)	64.38 (1.30)	B	B	B	B	B	B	B	B	A	B	B	B	B	3	4	A
Black Howler Monkeys (Group 3)	40.85 (2.31)	40.86 (2.47)	40.86 (2.47)	1	1	1	1	2	2	2	3	A	2	3	3	3	11	7	A
Bonnet Macaques (Group 1)	4.38 (0.27)	4.39 (.29)	4.39 (.29)	6	6	6	8	9	9	9	5	A	35	22	10	10	15	12	A
Bonnet Macaques (Group 2)	2.28 (0.19)	2.29 (.21)	2.29 (.21)	1	1	1	5	6	7	7	7	A	12	10	7	7	25	10	A
Bonnet Macaques (Group 3)	9.2 (2.49)	9.20 (2.62)	9.20 (2.62)	8	7	7	8	9	9	9	9	A	52	15	9	9	52	15	A
Bonobos	10.78 (2.43)	10.79 (2.49)	10.79 (2.49)	15	16	A	15	9	11	A	12	19	35	18	18	A	36	17	19
Campbell's Monkeys (Group 1)	NA	6.30 (1.24)	6.30 (1.24)	C	C	C	C	C	C	C	C	A	B	B	B	B	7	7	A
Campbell's Monkeys (Group 2)	NA	4.00 (.20)	4.00 (.20)	C	C	C	C	C	C	C	C	A	B	B	B	B	2	3	A
Chimpanzees (Group 1)	3.54 (0.76)	104.18 (65.55)	3333.63	23	22	22	24	22	21	21	21	7	116	29	27	27	144	30	7
Chimpanzees (Group 2)	6.95 (4.33)	14.95 (12.11)	14.95 (12.11)	1	1	1	2	3	5	5	2	A	B	B	B	B	11	16	A
Crested Macaques (Group 1)	2.14 (0.09)	7.72 (0.46)	7.72 (.46)	8	8	8	8	8	8	8	9	10	60	27	26	26	89	28	22

Crested Macaques (Group 2)	2.15 (0.14)	7.80 (.30)	7.80 (.30)	8	7	7	6	8	8	8	8	9	185	39	39	41	128	38	30
Diana Monkeys	NA	1.43 (.61)	1.43 (.61)	C	C	C	C	C	C	C	C	A	B	B	B	B	2	4	A
Indris (Group 1)	20.67 (1.63)	41.33	41.33	B	B	B	B	B	B	B	B	2	B	B	B	B	3	3	2
Indris (Group 2)	16.62 (6.73)	49.6	49.6	B	B	B	B	B	B	B	B	2	B	B	1	1	2	3	3
Indris (Group 3)	36.98 (1.56)	60.97	60.97	2	1	1	2	2	1	1	2	4	2	3	2	2	6	4	4
Indris (Group 4)	10.50 (4.61)	32.25	32.25	B	B	B	4	B	1	1	3	4	1	2	B	B	6	5	5
Indris (Group 5)	24.75 (4.49)	73.5	73.5	2	2	2	1	2	2	2	1	3	2	3	3	3	1	2	3
Indris (Group 6)	9.50 (1.75)	28.5	28.5	B	B	B	B	B	B	B	B	1	1	2	B	B	5	4	B
Indris (Group 7)	6.58 (1.21)	14.08	14.08	B	B	B	B	B	B	B	B	3	B	B	B	B	1	2	4
Japanese Macaques (Group 1)	NA	NA	133	C	C	C	C	C	C	C	C	A	78	20	A	17	A	A	A
Japanese Macaques (Group 2)	NA	NA	257.5	C	C	C	C	C	C	C	C	A	121	21	A	20	NA	NA	A
Japanese Macaques (Group 3)	3.37 (0.56)	3.37 (.59)	3.37 (.59)	3	5	5	8	6	7	7	9	A	7	10	B	B	27	22	A
Kinda Baboons	22.84 (12.92)	NA	35.55 (21.87)	7	7	7	A	3	3	3	A	A	57	36	33	33	A	A	A
Mongoose Lemurs (Group 1)	NA	14.37 (1.46)	NA	C	C	C	C	C	C	C	C	A	B	B	B	B	6	4	A
Mongoose Lemurs (Group 2)	NA	18.21 (1.84)	NA	C	C	C	C	C	C	C	C	A	B	B	B	B	4	4	A
Mountain Gorillas	33.34 (0.64)	45.84 (10.24)	504.25	6	6	6	7	5	7	7	6	A	15	12	9	8	26	12	A
Olive Baboons (Group 1)	NA	558.51	558.51	C	A	A	C	C	A	A	C	A	39	14	A	A	55	14	A
Olive Baboons (Group 2)	23.71 (10.62)	23.71 (10.78)	23.71 (10.78)	26	22	22	21	27	19	19	28	A	155	34	36	36	137	39	A
Olive Baboons (Group 3)	25.90 (7.47)	25.90 (7.75)	25.90 (7.75)	9	6	6	10	11	4	4	11	A	59	16	16	16	67	21	A
Red-fronted lemurs (Group 1)	NA	5.95 (1.01)	5.95 (1.01)	C	C	C	C	C	C	C	C	A	11	11	8	8	17	11	A
Red-fronted lemurs (Group 2)	NA	7.1 (0.49)	7.1 (0.49)	C	C	C	C	C	C	C	C	A	2	3	B	B	7	5	A
Red-fronted lemurs (Group 3)	NA	6.05 (0.26)	6.05 (0.26)	C	C	C	C	C	C	C	C	A	9	8	7	7	30	11	A
Red-fronted lemurs (Group 4)	NA	5.94 (1.57)	5.94 (1.57)	C	C	C	C	C	C	C	C	A	3	6	3	3	11	8	A
Red-Tailed Monkeys (Group 1)	3.52 (0.52)	2.60 (1.3)	2.60 (1.3)	3	B	B	6	4	B	B	7	6	5	6	B	B	28	9	6

Red-Tailed Monkeys (Group 2)	2.33 (0.25)	1.90 (.64)	1.90 (.64)	B	1	1	6	2	B	B	8	9	B	B	B	B	77	21	9
Ring-Tailed Lemurs (Group 1)	NA	16.8 (0.9)	16.8 (0.9)	C	A	A	C	C	A	A	C	A	59	12	A	A	19	12	A
Ring-Tailed Lemurs (Group 2)	NA	23.79 (.68	23.79 (.67	C	A	A	C	C	A	A	C	A	31	9	A	A	14	9	A
Ring-Tailed Lemurs (Group 3)	NA	19.90 (1.85)	19.90 (1.85)	C	A	A	C	C	A	A	C	A	42	10	A	A	16	10	A
Ring-Tailed Lemurs (Group 4)	NA	18.26 (.41)	18.26 (.41)	C	A	A	C	C	A	A	C	A	87	17	A	A	13	13	A
Ring-Tailed Lemurs (Group 5)	NA	13.60 (4.01)	13.60 (4.01)	C	A	A	C	C	A	A	C	A	65	13	A	A	18	11	A
Sooty Mangabeys	6.27 (1.98)	6.27 (2.02)	6.27 (2.02)	14	19	A	8	17	21	A	10	24	29	27	36	A	14	16	30
Verreaux's sifaka (Group 1)	65.00 (0.00)	41.75 (27.37) ,	41.75 (27.37)	1	1	1	1	2	2	2	2	A	6	4	2	2	5	5	A
Verreaux's sifaka (Group 2)	62.50 (1.50)	51.75 (21.20)	51.75 (21.20)	1	1	1	1	2	2	2	2	A	5	6	3	4	10	7	A
Verreaux's sifaka (Group 3)	59.50 (0.50)	44.25 (18.52)	44.25 (18.52)	1	1	1	1	2	2	2	2	A	6	4	4	4	9	6	A
Verreaux's sifaka (Group 4)	61.00 (0.00)	61.00 (0.00)	61.00 (0.00)	1	1	1	1	2	2	2	2	A	5	4	3	3	8	5	A
Verreaux's sifaka (Group 5)	54.50 (1.50)	38.00 (18.55)	38.00 (18.55)	1	1	1	1	2	2	2	2	A	9	6	4	4	9	7	A
Verreaux's sifaka (Group 6)	59.00 (0.00)	57.00 (3.46)	57.00 (3.46)	1	1	1	1	2	2	2	2	A	3	3	2	2	3	3	A
Verreaux's sifaka (Group 7)	33.00 (25.00)	44.25 (24.47)	44.25 (24.47)	2	2	2	1	1	1	1	2	A	3	3	NA	NA	8	7	A
Verreaux's sifaka (Group 8)	57.50 (0.50)	58.00 (1.00)	58.00 (1.00)	1	1	1	1	1	1	1	2	A	1	2	2	2	3	3	A
Verreaux's sifaka (Group 9)	27.06 (5.80)	27.07 (6.50)	27.07 (6.50)	B	B	B	B	B	B	B	B	A	3	4	3	B	7	5	A
Verreaux's sifaka (Group 10)	17.33 (9.19)	15.41 (10.86)	15.41 (10.86)	6	6	4	5	4	4	3	6	A	12	8	5	4	15	9	A
Verreaux's sifaka (Group 11)	31.91 (8.68)	25.53 (16.71)	25.53 (16.71)	2	2	2	2	1	1	1	2	A	4	4	4	B	6	4	A
Verreaux's sifaka (Group 12)	17.66 (8.12)	13.25 (11.11)	13.25 (11.11)	5	5	4	5	3	4	2	5	A	12	7	5	B	24	8	A
Verreaux's sifaka (Group 13)	27.60 (1.30)	27.60 (1.46)	27.60 (1.46)	4	4	3	4	3	2	1	4	A	5	5	4	B	10	5	A
Verreaux's sifaka (Group 14)	14.63 (7.86)	11.97 (9.53)	11.97 (9.53)	6	6	4	6	5	4	4	6	A	15	8	6	4	30	11	A

Spider Monkeys (Group 1)	8.94 (0.70)	9.11 (.70)	9.11 (.70)	3	4	4	6	4	8	8	6	A	5	6	9	9	31	19	A
Spider Monkeys (Group 2)	12.91 (4.43)	12.91 (4.55)	12.91 (4.55)	1	B	B	6	1	B	B	5	A	B	B	4	4	16	14	A
Vervet Monkeys (Group 1)	15.27 (3.63)	14.85 (3.92)	14.85 (3.92)	1	2	2	3	1	2	2	3	13	13	21	25	25	39	37	13
Vervet Monkeys (Group 2)	NA	86.42 (22.36)	86.42 (22.36)	C	C	C	C	C	C	C	C	B	189	29	33	B	427	34	35
Vervet Monkeys (Group 3)	NA	89.89 (31.58)	89.89 (31.58)	C	C	C	C	C	C	C	C	B	44	10	12	B	59	12	11
Western Gorillas	161.00 (139.55)	NA	161.06 (152.87)	4	4	4	B	4	4	4	B	A	9	5	4	4	B	B	A
White-Faced Capuchins (Group 1)	NA	11.17 (1.23)	NA	C	C	C	C	C	C	C	C	A	B	B	B	B	27	14	A
White-Faced Capuchins (Group 2)	NA	9.42 (1.48)	NA	C	C	C	C	C	C	C	C	A	B	B	B	B	24	13	A
White-Faced Capuchins (Group 3)	NA	8.15 (1.87)	NA	C	C	C	C	C	C	C	C	A	B	B	B	B	21	14	A
Yellow Baboons (Group 1)	NA	5.43 (1.20)	580	C	A	A	C	C	A	A	C	A	660	46	A	A	258	45	A
Yellow Baboons (Group 2)	NA	4.43 (1.08)	480.4	C	A	A	C	C	A	A	C	A	556	40	A	A	186	40	A
Yellow Baboons (Group 3)	NA	3.67 (1.00)	515.3	C	A	A	C	C	A	A	C	A	878	59	A	A	298	55	A
Yellow Baboons (Group 4)	NA	4.77 (0.99)	499.6	C	A	A	C	C	A	A	C	A	624	46	A	A	283	45	A
Yellow Baboons (Group 5)	NA	3.65 (1.09)	521.3	C	A	A	C	C	A	A	C	A	1431	70	A	A	328	68	A
Geladas (Group 1)	6.5 (2.10)	6.5 (2.10)	6.5 (2.10)	B	B	B	B	B	B	B	B	5	B	B	B	B	28	11	4
Geladas (Group 2)	2.08 (0.11)	2.08 (0.11)	2.08 (0.11)	B	2	2	1	1	1	1	1	3	B	B	B	B	20	16	B
Geladas (Group 3)	5.5 (1.70)	5.5 (1.70)	5.5 (1.70)	5	3	3	9	3	4	4	7	12	8	8	B	B	61	25	12
Geladas (Group 4)	3.56 (0.32)	3.56 (0.32)	3.56 (0.32)	B	B	B	B	B	B	B	B	3	B	B	B	B	14	6	3
Geladas (Group 5)	2.45 (0.24)	2.45 (0.24)	2.45 (0.24)	1	B	B	3	1	B	B	2	B	2	4	3	3	21	14	B
Geladas (Group 6)	NA	0.83 (.40)	0.83 (.40)	B	B	B	B	B	B	B	B	B	1	2	B	B	5	7	B
Geladas (Group 7)	NA	0.96 (.09)	0.96 (.09)	B	B	B	B	B	B	B	B	B	B	B	B	B	6	7	B
Geladas (Group 8)	7.15 (2.24)	7.15 (2.24)	7.15 (2.24)	7	5	5	9	5	4	4	9	8	14	12	8	8	56	14	9
Geladas (Group 9)	5.33 (0.62)	5.33 (0.62)	5.33 (0.62)	B	B	B	B	B	B	B	B	2	B	B	B	B	7	4	2
Geladas (Group 10)	11.25 (1.60)	11.25 (1.60)	11.25 (1.60)	1	2	2	3	1	1	1	3	3	1	2	B	B	18	6	4
Geladas (Group 11)	9.35 (1.60)	9.35 (1.60)	9.35 (1.60)	3	B	B	4	3	B	B	3	4	4	5	B	B	21	6	4
Geladas (Group 12)	13.5 (0.57)	13.5 (0.57)	13.5 (0.57)	4	2	2	5	5	2	2	6	B	7	8	B	B	37	15	B
Geladas (Group 13)	12.82 (3.51)	12.82 (3.51)	12.82 (3.51)	2	1	1	6	1	1	1	4	B	B	B	B	B	46	17	B

Geladas (Group 14)	3.1 (0.51)	3.1 (0.51)	3.1 (0.51)	B	B	B	B	B	B	B	B	4	B	B	2	2	12	8	4
Geladas (Group 15)	4.42 (0.37)	4.42 (0.37)	4.42 (0.37)	B	B	B	B	B	B	B	B	B	B	B	B	B	24	12	B
Geladas (Group 16)	2.78 (0.19)	2.78 (0.19)	2.78 (0.19)	B	B	B	B	B	B	B	B	7	B	B	B	B	27	13	6
Geladas (Group 17)	3.5 (0.00)	3.5 (0.00)	3.5 (0.00)	B	B	B	B	B	B	B	B	2	B	B	B	B	10	7	2
Geladas (Group 18)	10.37 (2.29)	10.37 (2.29)	10.37 (2.29)	B	B	B	B	B	B	B	B	4	2	3	B	B	15	6	4
Geladas (Group 19)	10.45 (3.12)	10.45 (3.12)	10.45 (3.12)	B	B	B	B	B	B	B	B	B	B	B	B	B	25	9	B
Geladas (Group 20)	14.5 (0.54)	14.5 (0.54)	14.5 (0.54)	B	B	B	B	B	B	B	B	B	B	B	B	B	12	5	B
Geladas (Group 21)	2.29 (0.17)	2.29 (0.17)	2.29 (0.17)	B	B	B	B	B	B	B	B	5	B	B	B	B	22	12	4
Geladas (Group 22)	3.47 (0.24)	3.47 (0.24)	3.47 (0.24)	2	3	3	6	2	4	4	5	10	2	4	7	7	63	17	10
Geladas (Group 23)	8.16 (0.48)	8.16 (0.48)	8.16 (0.48)	1	B	B	7	B	1	1	6	B	B	B	B	B	33	14	B
Geladas (Group 24)	9.5 (0.31)	9.5 (0.31)	9.5 (0.31)	B	B	B	B	1	B	B	B	B	B	B	B	B	23	11	B
Geladas (Group 25)	2.84 (0.51)	2.84 (0.51)	2.84 (0.51)	1	B	B	2	1	B	B	2	8	B	B	B	B	15	12	B
Geladas (Group 26)	6.25 (0.82)	6.25 (0.82)	6.25 (0.82)	B	B	B	B	B	B	B	B	5	B	B	B	B	27	9	5
Geladas (Group 27)	5.6 (1.61)	5.6 (1.61)	5.6 (1.61)	3	3	3	4	1	1	1	4	4	3	4	B	B	26	12	4
Geladas (Group 28)	3.33 (0.11)	3.33 (0.11)	3.33 (0.11)	1	B	B	B	B	B	B	B	3	B	B	B	B	6	6	B
Geladas (Group 29)	3.32 (1.85)	3.32 (1.85)	3.32 (1.85)	B	B	B	B	B	B	B	B	7	B	B	B	B	34	14	7
Geladas (Group 30)	2.43 (0.56)	2.43 (0.56)	2.43 (0.56)	B	B	B	B	B	B	B	B	7	B	B	B	B	24	10	9
Geladas (Group 31)	4.55 (1.38)	4.55 (1.38)	4.55 (1.38)	2	1	1	8	2	1	1	8	10	B	B	B	B	40	17	7
Geladas (Group 32)	13.75 (2.10)	13.75 (2.10)	13.75 (2.10)	5	3	3	7	4	3	3	7	B	7	7	5	5	51	16	B
Geladas (Group 33)	5.00 (0.39)	5.00 (0.39)	5.00 (0.39)	B	B	B	B	B	B	B	B	8	4	6	B	B	43	20	9
Geladas (Group 34)	NA	1.32 (0.99)	1.32 (0.99)	B	B	B	B	B	B	B	B	B	B	B	B	B	8	10	B
Geladas (Group 35)	3.30 (0.79)	3.30 (0.79)	3.30 (0.79)	B	B	B	B	B	B	B	B	B	B	B	B	B	10	6	B
Geladas (Group 36)	NA	0.50 (0.00)	0.50 (0.00)	B	B	B	B	B	B	B	B	B	B	B	B	B	2	2	B
Geladas (Group 37)	2.60 (0.12)	2.60 (0.12)	2.60 (0.12)	B	B	B	B	B	B	B	B	B	B	B	B	B	14	10	B
TOTAL				251	232	191	291	256	241	205	310	240	6171	976	487	408	4388	1423	312

Note: A= No data as data not collected, or not collected in a form that could be made consistent with our other datasets

B= Doesn't occur in species/ insufficient data collected to meet minimum criteria for inclusion in measure

C= No given/received tolerance measures calculated as didn't have the flee/submission data to calculate dominance rank and/or vocal rate data

Appendix 3 – Ethograms

Table A

Ethograms of aggressive behaviours included for each species, and whether the behaviour is of high intensity (defined as including physical contact).

Species	**Aggression Type**	**Definition**	**High Intensity? (y/n)**
Assamese macaques	Display	Only facial displays (e.g., open mouth threat, stare) or aggressive vocalizations (e.g., growl) are used by the aggressor	N
	Motion	The aggressor moves aggressively (e.g., lung, chase) towards the victim (can also include aggressive facial displays and vocalizations by the aggressor)	N
	Slap	Hits body part of victim	Y
	Bite	Seizes body part of victim with teeth	Y
	Push pull	The monkey grabs hold of another monkey's fur and skin, and makes a brief "shaking" movement.	Y
Barbary Macaques	Lunge	The monkey makes a sudden intense movement towards another monkey. It does not move over a large distance. Sometimes only the upper body is moved.	N
	Charge	A monkey pursues another monkey for less than 5 metres.	N
	Chase	The monkey pursues another monkey partner at high speed	N

	Slap	The monkey forcefully grabs another monkey with it's hands and/or legs.	Y
	Push Pull	The monkey grabs hold of another monkey's fur and skin, and makes a brief "shaking" movement.	Y
	Jump On	A monkey jumps onto another.	Y
	Bite	The monkey seizes body part of another monkey with teeth	Y
	Ground slap	The monkey hits the ground with an opened hand in short, intense movements.	N
	Run Towards	A monkey runs towards another monkey in order to displace them. This usually occurs to displace a subordinate from a food source	N
	Get involved	The monkey runs towards an ongoing conflict to get involved. Often you cannot follow fast enough, but you know that your focal animal takes part in the conflict.	Unknown
	Aggression Unknown	Monkey known to be in aggressive interaction but behaviour not observed.	Unknown
Black Howler Monkeys	Threat	shake branches and stare, show teeth (without approaching the victim)	N
	Chase	Pursuit of fleeing victim with physical contact but without biting or grasping brutally, generally with calls	Y
	Bite	Seizes body part of victim with teeth, risk of injuries	Y
Bonnet Macaques	Charge	Sudden rush towards target individual without pursuit	N

Chase	Pursuit of a target individual	N
Head-Jerking	Repeated swift movements of the head, usually vertically, while looking directly towards the recipient	N
Lunging	Sudden jump toward the recipient, followed by a swift return to the original position	N
Open-Mouth Threatening	Opening the mouth in rounded form along with slight forward head movements and followed by a rapid closing of the mouth, while looking directly at the recipient	N
Eye Flashing	Sudden widening of the eyes with raising of the eyebrows, usually displayed repeatedly, whjile looking directly at the recipient	N
Holding Down Roughly	Holding the recipient tightly and pushing her/him down towards the ground without any release	Y
Slapping	Sudden quick movement of the palm, making forcible contact with the recipient’s cheek/body/head	Y
Biting Hard	Holding the recipient tightly and biting with the mouth fully closed and with the teeth often embedded in a recipient’s body part	Y
Holding Down Roughly	Holding the recipient tightly and pushing her/him down towards the ground without any release	Y
Slapping	Sudden quick movement of the palm, making forcible contact with the recipient’s cheek/body/head	Y

Bonobos	Threats	Directed arm raises, lunges, threat barks which include victim fleeing or retracting from aggression	N
	Directed branch displays	Dragging/shaking branch in direction of the target, may include fleeing/retraction by victim	N
	Chase	Pursuing the target who flees	N
	Biting	Seizing a part of the body with teeth	Y
	Hit/Slap	Striking the victim with the hand	Y
	Jumping on	Stamping on victim with feet	Y
	Beating	Repeated kicking/punching of victim	Y
Campbell Monkeys	Biting	Seizes body part of victim with teeth	Y
	Hitting	Sharply strikes body part of victim	Y
	Pushing violently	Violently pushing another individual away (with hand/arm or foot)	Y
	Pushing Away with Arms	This is the same behaviour as above but more gentle, the individual is pushing another one away with his arm/hand or foot	Y
	Chase	Pursuit of fleeing victim (without grasping or bitting)	N
	Threat (postural and/or facial)	This goes from mild threat (e.g. shaking branches and staring) to gradually more strong threats (rising the eyebrows or showing teeth and head bobbing) without ever approaching/grasping.bitting the victim	N
Crested macaques	rubbing ground	Forward sliding movement of the hand on a surface	N

	bite	Seizes body part of victim with teeth	Y
	chase	Pursuit of fleeing victim	N
	displacement	Approach or contacts an individual which simultaneously moves away	N
	grab	Seizes body part of victim with hand	Y
	hit/slap/push	Sharply strikes body part of victim or exerts pressure against victim with hand	Y
	missed hit	Attempts to strike victim but no contact is made	N
	stamp	Abrupt landing with stiff limbs following a run	N
	harassment	Multiple individuals repeatedly displaying aggressive behaviours towards a single individual, usually grabs, bites, slaps.	Y
	stare	Visual fixation on another individual	N
	lunge	Jump or short run toward another	N
	low threat (jaw movement, often with hard grunt)	Head trust forward and the lower jaw is moved up and down rapidly and rythmically. The mouth is closed or slightly open and the lips slightly protrude. The teeth may be knocked together, and the scalp may be retracted and ears flattened	N
	middle threat (half open mouth, often with rattle)	The mouth is slightly open with corners drawn back, the lower lip may be retracted and the teeth are partly visible	N
Chimpanzees	Attack 1	Any quick contact aggression (kick, slap, etc.) made in passing	Y

	Attack 2	Any extended pounding, kicking, dragging, etc. lasting less than 30 seconds and not resulting in serious wounding	Y
	Attack 3	Any extended pounding, kicking, dragging, etc. lasting more than 30 seconds and not resulting in serious wounding	Y
	Chase	Individual pursues a specific fleeing conspecific, who is generally screaming	N
	Charge	Fast locomotion towards other individuals, but no contact or deviation from trajetory to chase a specific individual.	N
	Display/ Threat	Range of threatening behaviours (throwing objects, foot stomps, arm waves, branch shakes) with or without movement towards victim	N
Diana monkeys	Biting	Seizes body part of victim with teeth	Y
	Hitting	Sharply strikes body part of victim	Y
	Pushing violently	Violently pushing another individual away (with hand/arm or foot)	Y
	Pushing Away with Arms	This is the same behaviour as above but more gentle, the individual is pushing another one away with his arm/hand or foot	Y
	Chase	Pursuit of fleeing victim (without grasping or bitting)	N
	Threat (postural and/or facial)	This goes from mild threat (e.g. shaking branches and staring) to gradually more strong threats (rising the eyebrows or showing teeth and head boobing) without ever approaching/grasping.bitting the victim	N

Geoffrey's Spider Monkeys	Visual/Vocal Threat	Without approaching the victim, aggressor shakes branches and stares, growls, shows teeth or produces open mouth threat	N
	Piggy-back threat	2+ individuals pile on top of one another in a threat display	N
	Chase with contact	Pursuit of fleeing victim, with physical contact	Y
	Chase without contact	Pursuit of fleeing victim, without physical contact	N
	Displacement	Individual takes place of another	N
	Lunge	Aggressor rapidly advances torwad another and stops	N
	Bite	Aggressor seizes victims' body part with teeth (risk of injuries)	Y
	Slap	Aggressor hits part of victim's body	Y
	Grab	Aggressor seizes part of victim's body	Y
Geladas	Vocal/Visual threats (i.e., threat grunts),	Threat grunts or eye-brow raise	N
	Chase	Pursuit of a fleeing victim	N
	Bite	Seizes body part of victim with teeth	Y
	Hit	Sharply strikes body part of victim with hand	Y
Indris	Charge / dominance display:	Fast locomotion towards other individuals.	N

	Chase:	Individual pursues a specific fleeing conspecific, who may rarely scream	N
	Hit	Sharply strikes body part of victim with hand	Y
	Slap	Sharply strikes body part of victim with open hand	Y
	Biting	Seizes body part of victim with teeth	Y
	Grabbing	Seizes body part of victim with hands	Y
	Displacement	Individual takes place of another	N
Japanese macaques	Chase/Charge	Pursuit of fleeing victim	N
	Grab	The monkey forcefully grabs another monkey with its hands and/or legs.	Y
	Slap	The monkey hits another monkey with an opened hand.	Y
	Push and pull	The monkey grabs hold of another monkey's fur and skin, and makes a brief "shaking" movement.	Y
	Bite	The monkey seizes another monkey with teeth in the skin and fur.	Y
	Run towards	A monkey runs towards another monkey in order to displace them. This usually occurs to displace a subordinate from a food source.	N

Open Mount	The monkey’s mouth is opened, the jaws are tensed, and the lips cover the teeth. The eyes are wide open; it stares at the monkey it is angry with. This is often accompanied by a head bob, and can be accompanied by a pant vocalization.Body of the monkey is tense; usually the head is lowered and stuck forward. Usually the animal has its hair standing up. The eyes are wide open; it stares at the monkey it is angry with. The ears are held out away from the head, sometimes the eyebrows are lifted. The monkey’s mouth is opened, the jaws are tensed and the lips are pulled up, so that teeth and sometimes gums are shown.	N
Stare	Stare - The body of the monkey is tense; usually the head is lowered and stuck forward. Usually the animal has its hair standing up. The eyes are wide open; it stares at the monkey it is angry with. The ears are held out away from the head, sometimes the eyebrows are lifted.	N
Lift	The monkey looks at another monkey; the eyebrows and scalp are lifted, sometimes several times. The monkey will usually have its eyes half closed. The ears are flattened against the head.	N
Lunge	Lunge - The monkey makes a sudden intense movement towards another monkey. It does not move over a large distance. Sometimes only the upper body is moved.	N
Bite	Seizes body part of victim with teeth	Y

Kinda Baboons	Hit	Sharply strikes victim with hand	Y
	Grab	Seizes body part of victim with hand	Y
	Slap	Sharply strikes victim with open hand	Y
	Hold Down	Physically holds body (or body part, e.g. head) of victim onto ground	Y
	Eye flash	Quickly opens/closes eyes so as to expose bright eyelids; often association with raised eyebrows and widened eyes	N
	Shake Branch	Takes hold of branch and sharply moves it around	N
	Lunge	Quickly and sharply moves body <5 meters of another individual, <5 seconds	N
	Head Bob	Extends neck up/down quickly, often making eye contact with victim	N
	Chase	One individual runs after another at >5 meter distance for >5 seconds	N
Mountain Gorillas	Hit	Sharply strikes body part of victim with hand	Y
	Kick	Sharply strikes body part of victim with foot	Y
	Grab	Seizes body part of victim with hand	Y
	Chase	Pursuit of fleeing victim	N
	Lunge	Sharp sudden movement towards victim	N
	Bite	Seizes body part of victim with teeth	Y

	Drag	Takes hold of and pulls victim to another location	Y
Olive Baboons	Grab	Seizes body part of victim with hand	Y
	Push	Exerts pressure against victim with hand to displace them	Y
	Pull	Takes hold of and moves victim towards themselves	Y
	Bite	Seizes body part of victim with teeth	Y
	Slap	Sharply strikes victim with hand	Y
	Hit	Sharply strikes victim with open hand	Y
	Supplant*	Moves towards and takes place of victim who moves away	N
	Chase	Pursuit of fleeing victim	N
	Threat*	eyebrow raise (raises eyebrows while looking at the recipient) and/or a head bob (while looking at recipient, quickly moves its head down and then back up again) and/or molar grinding	N
	Lunge at*	Putting one or both forelimbs on the ground in the direction of the aggressee while keeping its hindlimbs in the same place	N
Red-Fronted Lemurs	Displacement	Moves towards and takes place of victim who moves away	N
	threat	sudden abrupt turn towards another animal within 1m	N
	batting	manually strike partner	Y

	biting	Seizes body part of victim with teeth	Y
	wrestling	at least two individuals are entangled with each other	Y
	Chase	Pursuit of fleeing victim	N
Red-Tailed Monkeys	Lunge	a swift pounce or swipe, not moving more than one body length	Y
	Threaten	a face with bared teeth, often accompanied by jerks of the head to alternating sides and a crouched posture	N
	Growl	a low-pitched call given only in situations where the vocalizer is exhibiting aggression toward another animal	N
	Hit/slap	a fast-moving, brief, and forceful contact of the aggressor's arm and hand against a body part of the recipient	Y
	Chase	an individual rapidly pursues another individual for >1 body length	Y
	Bite	an individual grabs some part of another animal in its mouth, generally concurrent with other aggressive behaviors; unlike grooming which may involve eating ectoparasites from the skin of another animal, biting occurs during intensely aggressive interactions and evokes a strong response from the recipient	Y
	Supplant	an individual approaches another at a slow or moderate pace; the approached animal moves away - also at a slow or moderate pace - while the approacher moves into the space occupied by the departing individual	N

Ring-Tailed Lemurs	Bite	orally seize or slash partner's body part	Y
	Cuff	manually strike partner (or attempt)	Y
	Grab	rapidly seize partner's pelage or body part using two hands	Y
	Push	Thrust away aggressively with hands or arms	Y
	Nose Poke	Push away aggressively with nose	Y
	Lunge	thrust upper torso or whole body toward nearby partner	N
	Displace	To approach a conspecific in a way that causes them to defensively move away	N
	Chase	sprint in pursuit of fleeing partner (> 5 m)	N
	Stare	When one animal looks at another and elicits submissive behavior (vocalizations or a withdraw) just by glancing	N
	Attack	one or more animals biting, cuffing, etc. another animal with high intensity (usually, rolling around on floor; one or more animals have an individual pinned to ground)	Y
	Stalk	deliberately approach partner using rigid posture and movements	N
Sootey Mangabeys	Stare	The actor raises his eyebrows and his forehead staring directly at the target animal, he can lower and lift his head while staring.	N
	Stare and lunge	After the stare, the actor quickly rushes towards the target animal, but stops before reaching it. At this moment the aggressor lowers his shoulders as if he was preparing to jump forwards.	N

	Chase:	Individual pursues a specific fleeing conspecific	N
	Hit	Sharply strikes body part of victim with hand	Y
	Kick	Sharply strikes body part of victim with foot	Y
	Slap	Sharply strikes body part of victim with open hand	Y
	Pounding	Repeatedly striking victim with closed fist	Y
	Gripping	Takes hold of other's fur	Y
Verreaux's Sifaka	Biting	Seizes body part of victim with teeth	Y
	Cuff/Grab	Actor manually strikes or holds conspecific	Y
	Chase	Actor moves quickly (>1m/s) towards a conspecific (B) who moves away from the actor. Actor follows B in this away from B’s original location.	N
	Displace	Actor moves towards conspecific (B), who immediately leaps away. The actor then occupies the location previously held by B.	N
	Threat*	Sudden abrupt turn to conspecific within 1m	N
Vervet monkeys	Lunge	Aggressor quickly and suddenly moves in the direction of another individual, causing this individual to move away or cower	N
	Chase	Running after another individual who is fleeing	N

	Threat	Popping up the eyelids, exposing the white above the eyes, sometimes combined with attack; or aggressive vocalisations (eg., chutters, barks, grunts)	N
	Slap	Aggressor hits any body part of another individual with palm of hand	Y
	Grab	Catching another individual with the hand	Y
	Bite	Grabbing another individual with their mouth/teeth	Y
Western Gorillas	Vocal Threat	cough (or pig) grunt is an agonistic vocal threat used by all gorilla species	N
	Pretend Charge	Assuming the position for a charge, and moving suddenly with the upper body without following up/ no real moving toward the victim (kind of jump the gun)	N
	Arm Movement	Waive/Lunge the arm toward the other	N
	Charge	run towards the victim generally while roaring or screaming.	N
	Chase	Pursuit of fleeing victim	N
	Display	locomotor: few steps followed by staing up on hind limbs and chest beating; postural: in travel pose with puffy lips, piloerection, in some cases with herbs or leaves in mouth, showing his side	N
	Lunge	Move fast and suddenly toward another individual	N
	Scream/ roar	Mild vocal aggression signals with no charge	N

	Bite	Seizes body part of victim with teeth	Y
	Scratch	Drags nails across body part of victim	Y
	Forcing down	One individual goes over the other forcing him/her down with hands and body	Y
	Hitting	beating the other with fist or open hand	Y
Yellow Baboons	Raised brow or eyelid display	Display of unpigmented skin beneath eyebrows either by raising brow itself or tilting head dorsally; often accompanied by jutting forward of the head	N
	Open mouth face or attempted bite	Jaw held open, teeth not exposed or only slightly exposed, often accompanied by forward jutting of the head.	N
	Bobbed head and thorax	Abrupt, rapid raising and lowering of head and trunk; body may show a forward movement component.	N
	Ground slapped	Palm of hand or hands struck against ground, often audible.	N
	Lunged at	Forward leaping or jumping towards another individual; no lateral movement.	N
	Chomped or gave exaggerated chewing motions	Repeated and exaggerated chewing or grinding movements of the jaws, often with extreme lateral excursion, copious salivation and audible grinding.	N
	Gave threat yawn or directed gape	Directed gape or yawn-like moving, usually exposing canines.	N

Rubbed muzzle on substrate	Muzzle and chin rubbed laterally on ground or tree limbs. Often accompanied by gaping and chomping.	N
Hit or slapped	Rapid, open-handed striking or attempted striking of another individual	Y
Pushed	Open-handed shoving or attempted shoving of another individual.	Y
Grabbed	Closed-handed gripping of another individual, usually brief.	Y
Held down	Closed-handed gripping of another individual, forcing that individual against substrate, usually prolonged.	Y
Bite	Gripping another individual with teeth	Y
Walked at or ran at	Directed movement towards individual	N
Head flagged	Rapid repeated lateral head movements and/or eyelid flashing oriented first toward one individual and then another. May be accompanied by rapid full or partial closure of the eyelids producing flashes of unpigmented skin.	N
Low-pitched vocalizations	Vocalisations of low frequency produced in aggressive contexts, Eg., Grunt, roar, bellow, cough	N
Brush past	One animal (usually a male) walks briskly towards a second animal (usually a male) and then suddenly turns and walks away again just when he is very close. Often he literally brushes against the other animal.	Unknown

	Displacement	(1) when one animal moves steadily towards the spot where a second animal is sitting or standing, the second animal moves away when the first is less than five meters away, and the first comes to stand or sit, at least briefly, in the spot where second was. (2) when one animal moves steadily towards the spot where a second animal is sitting or standing, the second moves away when the first is within 5 m, and the first passes right through the spot where the second was. (3) When one animal is on a path that does not intersect with the position of a second animal but comes within one or two meters of it, and the second animal glances in the direction of the first and immediately moves away from its spot.	N

Note: Behaviours of unknown intensity were not included in calculation of intensity measures. Some datasets included behaviours involving stealing a resource (eg., ‘steal food’, ‘steal baby’). These were excluded as they do not constitute aggressive acts in themselves, but rather the source of the conflict. If aggressive behaviour occurred during, before or after stealing the resource, this behaviour was included.
*Equivalent behaviour not recorded in all groups of species.

Appendix 4 – Methods summary

Table A

Summary of data collection methods and bout definitions used across different datasets

Species	Fieldsite	Focal Length	Groom Method	Groom Inter-bout Interval	Aggression Method	Aggression Inter-bout interval	Frequency of Feeding Proximity scans
Assamese Macaques	Phu Khieo Wildlife Sanctuary, Thailand	40min	Focal	30sec	Focal	10sec	NA
Barbary Macaques	Middle Atlas mountains, Morocco	40min	Focal	30sec	Focal	30sec	NA
Black Howler Monkeys	Palenque National Park, Mexico	30mins	Focal	10sec	Focal	1min	NA
Bonnet Macaques	Bandipur National Park, Karnataka, India	15min	Focal and All-Occurrence	30sec	Focal	30 sec	NA
Bonobos	LuiKotale, Democratic Republic of Congo	15mins	Focal	30sec	Focal and All-Occurrence	30sec	Every 5 mins
Campbells Monkeys	Taï National Park, Ivory Coast	15mins	Focal	10sec	Focal	1min	NA
Chimpanzees	Kibale National Park, Uganda	15mins (vocal) 10 mins (groom)	Focal	1min	All-Occurrence	1min	Beginning and end of 15 min focals
Chimpanzees	Nyungwe National Park, Rwanda	Day-long follows; mean(sd) length: 8.63(2.38)hrs	Focal	30sec	Focal	30sec	NA
Crested Macaques	Tangkoko Nature Reserve, Sulawesi, Indonesia	30mins	Focal	30sec	Focal	30sec	Every 2 min

Diana Monkeys	Taï National Park, Ivory Coast	10mins	Focal	10sec	Focal	30sec	NA
Geladas	Simien Mountains National Park, Ethiopia	15mins	Focal	30sec	Focal	30sec	Every 5 mins
Geoffrey's Spider Monkeys	Otoch Ma'ax yetel Kooj protected area, Yucatan peninsula, Mexico	15min	Focal	10sec	Focal	1min	NA
Geoffrey's Spider Monkeys	Runaway Creek Nature Reserve, Belize	10mins	Focal	30sec	Focal and Ad-Lib	30sec	NA
Indris	Maromizaha Forest, Madagascar	5mins	All-Occurrence	30sec	All-occurrence	5mins	Every 5 mins
Japanese Macaques	Yakushima, Japan*	1hr	Focal	30sec	Focal and Ad-Lib	2sec	NA
Japanese Macaques	Yakushima, Japan*	10mins	NA	NA	Focal	10sec	NA
Kinda Baboons	Kasanka National Park, Zambia	30mins	NA	NA	Focal	30sec	NA
Mongoose Lemurs	Ankatsabe Forest, Madagascar	1 hour	Focal	30sec	NA	NA	NA
Mountain Gorillas	Bwindi Impenetrable National Park, Uganda	10-60mins	Focal	1min	All-Occurrence	30sec	NA
Olive Baboons	Laikipia, Kenya	15mins	Focal	30sec	Focal	30sec	NA
Olive Baboons	Gashaka Gumti National Park, Nigeria	NA	All-Occurrence	15mins	All-Occurrence	15mins	NA
Red fronted lemurs	Kirindy Forest, Madagascar	30 mins	Focal	30sec	Focal	30min	NA
Red-tailed monkeys	Kibale National Park, Uganda	10mins	Focal	30sec	Focal and Ad-Lib	30sec	Every 1 min

Ring Tailed Lemurs	Beza Mahafaly Special Reserve, Madagascar	NA	Focal	30sec	Focal	30sec	NA
Sooty Mangabeys	Taï National Park, Ivory Coast	1-6h	Focal	30sec	Focal	30sec	Every 15 mins
Verreaux’s Sifaka	Kirindy Forest, Madagascar	1 hour	Focal	30sec	Focal	30sec	NA
Verreaux’s Sifaka	Bezà Mahafaly Special Reserve, Madagascar	20mins	Focal	30sec	Focal	30sec	NA
Vervet Monkeys	Soetdoring Nature Reserve, South Africa	20mins	Focal	30sec	Focal and Ad-Lib	30sec	Every 4 mins
Vervet Monkeys	Mawana Game Reserve, South Africa	Length varies; mean (SD) 3.72 (0.95) hrs	Focal	30sec	Focal	30sec	Every 15 mins
Western Gorillas	Mondika Research Center, Congo	1h	NA	NA	Focal	1min	NA
White Faced Capuchins	Santa Rosa National Park, Costa Rica	10 min	Focal	30sec	All-Occurrence	30sec	NA
Yellow Baboons	Amboseli National Park, Kenya	10 min	Focal	30sec	All-Occurrence	10sec	NA

*Note: *Two different datasets were provided from the same fieldsite (groups comprised different individuals)*

Appendix 5 – Species summary

Table A

Dominance style and vocal measure values for all species included in sample; references provided for repertoires and any deviations from ours and McComb & Semple's (2005) criteria indicated by super-script.

		Dominance Style Measures						**Vocal Measures**				
Family	**Species**	**Dominance Style Score**	**Aggression DII**	**High Intensity Aggression**	**Counter-aggression**	**Groom DII**	**Feeding Proximity**	**Vocal Rate (N bouts/ hour)**	**Repertoire Size**	**Social Signals**	**Hierarchy-Related Signals**	**Repertoire Reference**
Hominidae	*Pan paniscus*	0.23	0.03	16.94%	A	0.41	8.86%	3.82	38	31	0	Bermejo & Omedes (1999)
	Pan troglodytes schweinfurthii	-0.48	0.04	50.53%	3.83%	0.32	17.95%	3.12	13	9	4	Slocombe & Zuberbuhler, (2010)
	Gorilla beringei beringei	-0.99	0.09	73.70%	11.88%	0.10	A	8.94	16	12	5	Harcourt, Stewart and Hauser, (1993)
	Gorilla gorilla gorilla	0.42	0.06	1.11%	24.24%	B	A	8.91	14	3	0	Salmi, Hammerschmidt & Doran-Sheehy (2013)
Cercopithecidae	*Cercocebus atys*	0.25	0.06	7.63%	A	0.35	9.19%	1.07	18	12	2	Range & Fischer (2004)
	Cercopithecus ascanius	0.07	0.13	B	B	0.31	42.39%	14.12	5	1	0	Marler (1973)[a]
	Cercopithecus campbelli	B	B	B	B	0.44	A	A	17	8	1	Lemasson & Hausberger (2011)[b]
	Cercopithecus diana	B	B	B	B	0.25	A	A	11	2	0	Candiotti, Zuberbuhler, Lemasson (2012)[b], Stephan & Zuberbuhler (2014); Stephan & Zuberbuhler (2016)[c]
	Chlorocebus pygerythrus	0.43	0.09	10.36%	27.09%	0.35	6.91%	1.72	25	7	3	Strushaker (1967)
	Macaca assamensis	-0.45	0.09	21.96%	5.29%	0.17	A	6.97	16	10	3	Kaewpanus, (2014)[d]
	Macaca fuscata yakui	-0.27	0.00	A	0.00%	0.43	A	11.57	34	23	16	Green (1975)
	Macaca nigra	-0.27	0.03	16.43%	5.89%	0.27	16.39%	6.92	11	6	0	Panggur (2013)[d]
	Macaca radiata	-0.51	0.04	22.05%	0.60%	0.22	A	1.73	21	11	7	Hohmann (1989)
	Macaca sylvanus	0.06	0.09	18.47%	17.10%	0.29	A	0.33	14	5	0	Fischer & Hammerschmidt (2002)
	Papio anubis	-0.34	0.09	16.87%	0.00%	0.22	A	5.81	7	4	1	Inglis (2014)
	Papio cynocephalus	-0.63	0.02	A	A	0.28	A	A	7	4	1	Chiou (2013); Hammerschmidt & Fischer, 2018[d,e]
	Papio kindae	-0.21	0.02	10.37%	3.18%	A	A	2.32	E	E	E	E
	Theropithecus gelada	0.16	0.13	23.36%	4.22%	0.40	21.73%	10.51	14	7	3	Gustison, Roux & Bergman (2012)
Platyrrhini	*Alouatta pigra*	1.13	0.33	51.67%	70.00%	0.30	A	0.31	12	4	0	Briseño-Jaramillo et al., (2017)
	Ateles geoffroyi	-0.18	0.40	100.00%	13.24%	0.23	A	8.43	24	12	5	Eisenberg (1976)
	Cebus imitator	B	B	B	B	0.24	A	NA	20	10	5	Gros-Louis et al., (2008)
Lemuroidea	*Eulemur mongoz*	B	B	B	B	0.42	A	7.57	9	6	1	Gamba et al., (2015)[a]
	Eulemur rufifrons	0.48	0.18	38.85%	11.78%	0.50	A	A	10	4	2	Gamba et al., (2015)[a,e]
	Indri indri	0.67	0.31	68.89%	26.11%	0.47	13.99%	0.32	18	5	0	Maretti et al., (2010); Gamba et al,. (in prep)[c]
	Lemur catta	0.71	0.08	A	A	0.50	A	A	22	14	4	Macedonia (1993)
	Propithecus verreauxi	D	0.13	68.00%	41.00%	0.25	A	4.93	D	D	D	D

Note: Reasons for exclusion of measures for species provided by the following key:

A= No data as data not collected, or not collected in a form that could be made consistent with our other datasets

B= Doesn't occur in species/ insufficient data collected to meet minimum criteria for inclusion in measure

C= No given/received tolerance measures calculated as didn't have the flee/submission data to calculate dominance rank and/or vocal rate data

D= No published repertoire available for species (Dominance Style composite only used for repertoire analyse)

E= Excluded from repertoire analyses because no phylogenetic information available for species.

We followed guidelines set out by Mccomb & Semple (2005) as closely as possible when selecting species repertoires. Typically there was just one available for a species, but where there were multiple options we included the one selected as the best characterisation of the species' repertoire by the author in the current study who provided data for the species. However it was not possible to find a single published repertoire documenting all call types for males and females for all species included in our sample. There are some exceptions to the criteria for repertoire selection and call categorisation set out in the main text, with deviations from criteria indicated by the superscript:

[a] Published paper didn't provide enough detail about contexts of calls, so the contexts were provided through personal communication with the paper's author

[b] Females only (however these species only included in one analyses as they only had data for one dominance style measure; Groom DII)

[c] Combined more than one repertoire; Diana monkeys; predatory and non-predatory calls, Indri lemurs; song and non-song calls)

[d] Unpublished repertoire, researchers contributing data for the species agreed that they accurately reflect vocal repertoire of species

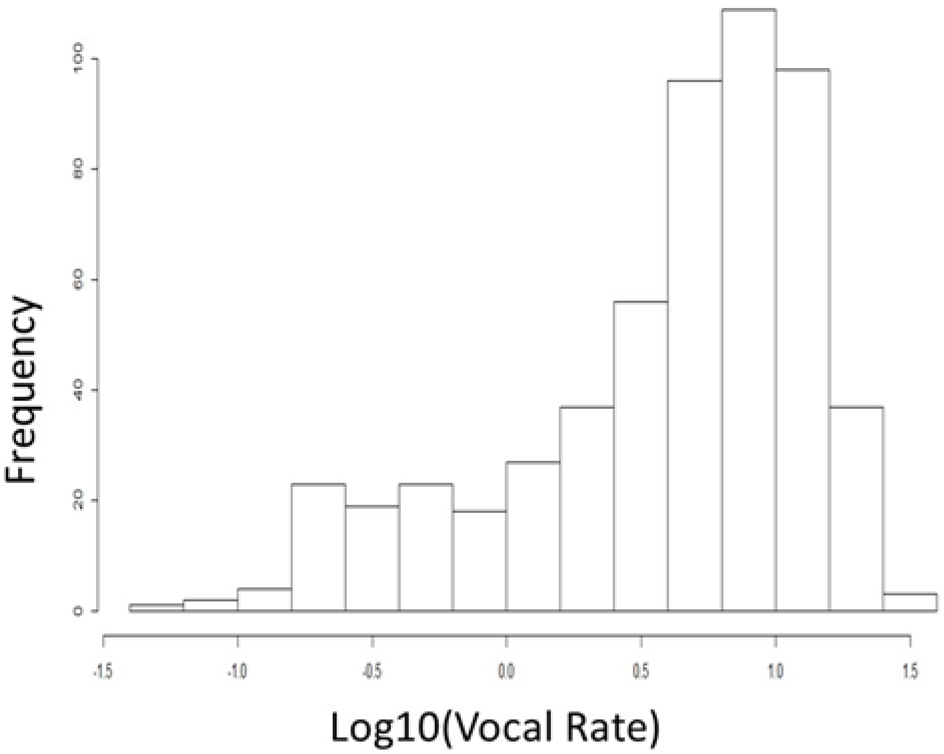
[e] Used published repertoire of sister species, authors contributing data for the species agreed that they accurately reflect vocal repertoire; for yellow baboons; we included any calls from two sister species that data contributors agreed were present; scream, bark, wahoo, grunt, roar-grunt, copulation call, geck

[f] Repertoire mentioned vocalisation that might exist but not heard in study period; included these as author contributing data for project agreed that it is present in species; 'growls' in red-tailed monkeys

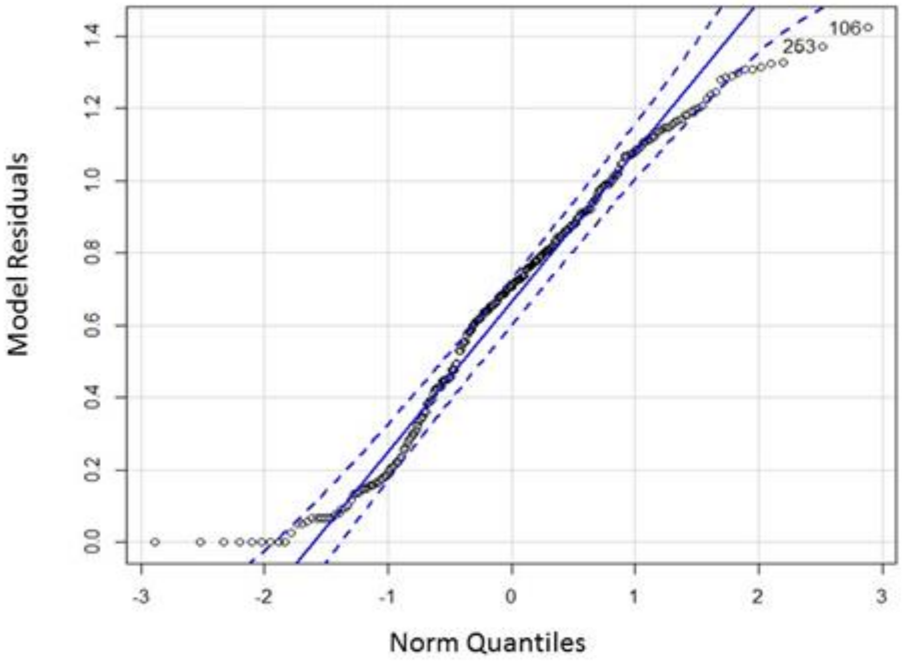
Appendix 6 – Sample diagnostic plots

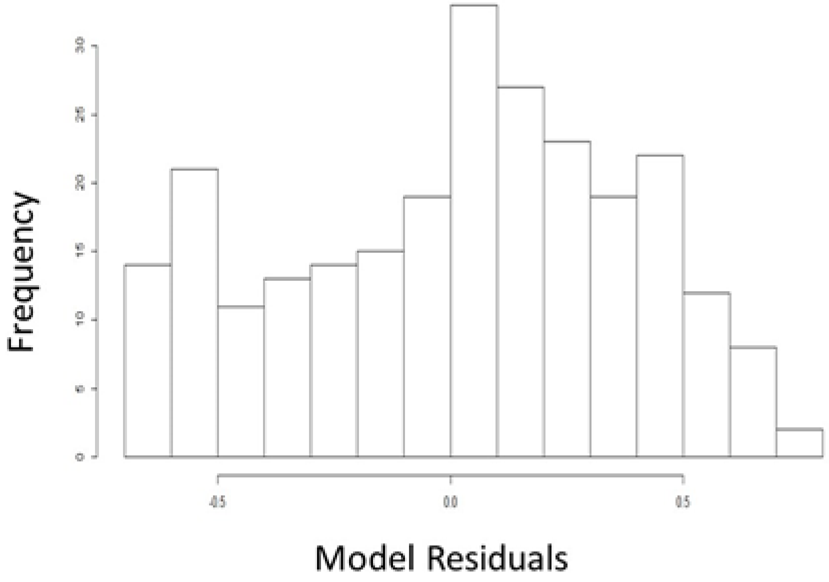
Below are the plots associated with our model examining whether given tolerance Aggression DII predicts vocal rate (as reported in Table C). This model used a Gaussian distribution with a log10 transformation on the dependent variable, and is a typical example of the MCMC models used, as some plots indicate a good fit whereas others do not.

1) Distribution of the dependent variable (log10 transformation on vocal rate) showed an imperfect fit to normal distribution.

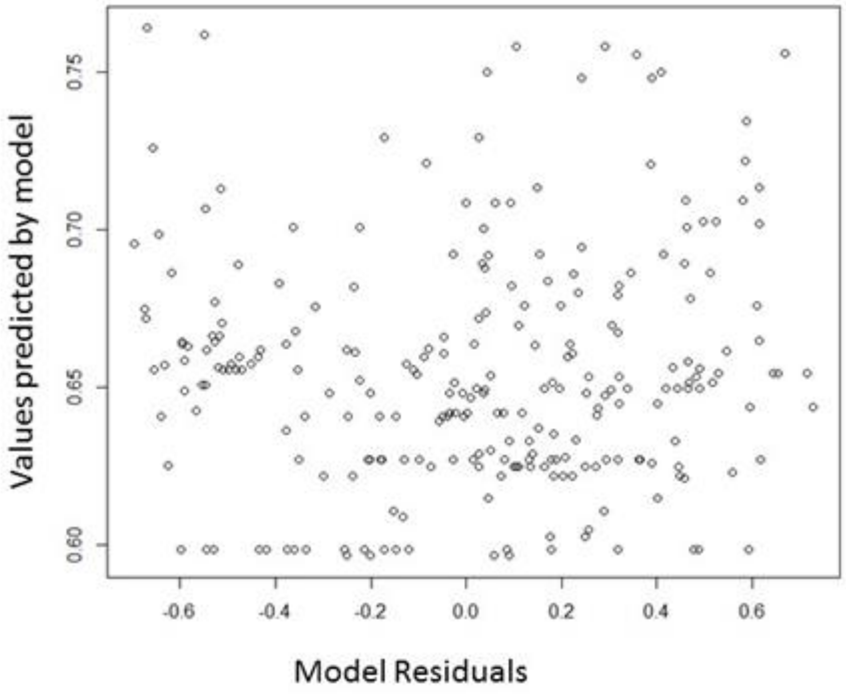


2) Distribution plot of the model residuals also displayed an imperfect fit to a normal distribution.

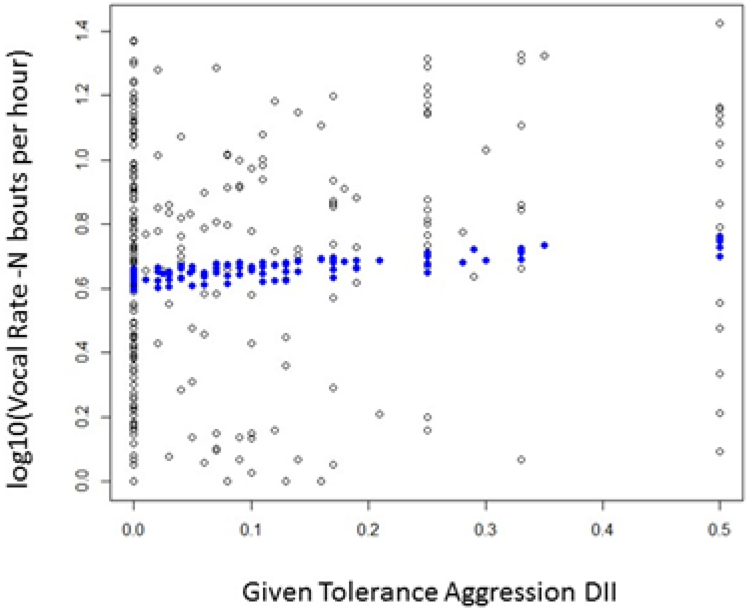




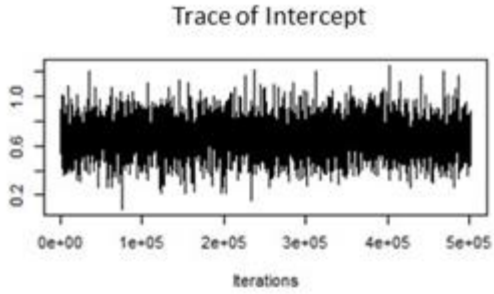
3) Plot displaying the residuals against the fitted values of the model showing no clear patterning suggestive of heteroscedasticity.

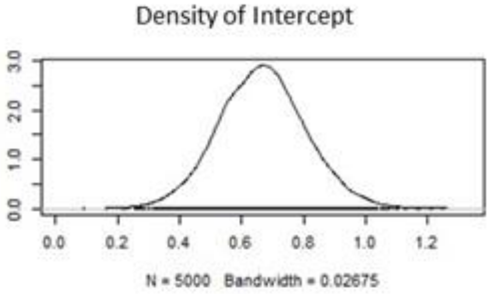


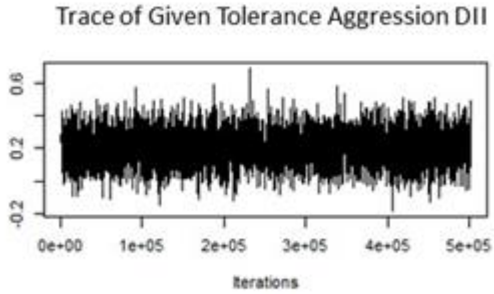
4) Plot of dependent versus independent variable with predicted values from the model overlaid (in blue)

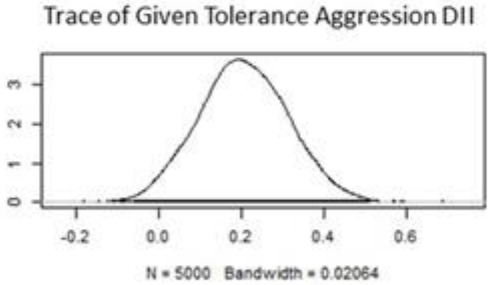


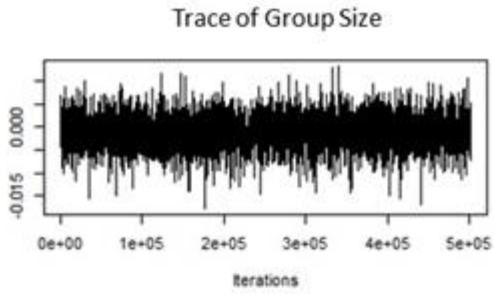
5) The chain and density plots suggested no problems with model convergence.

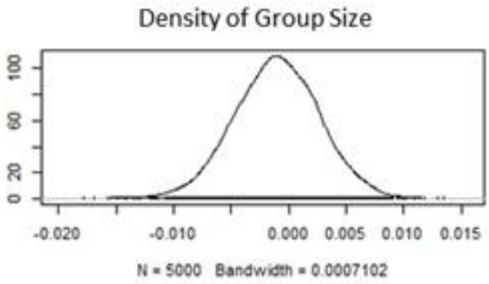


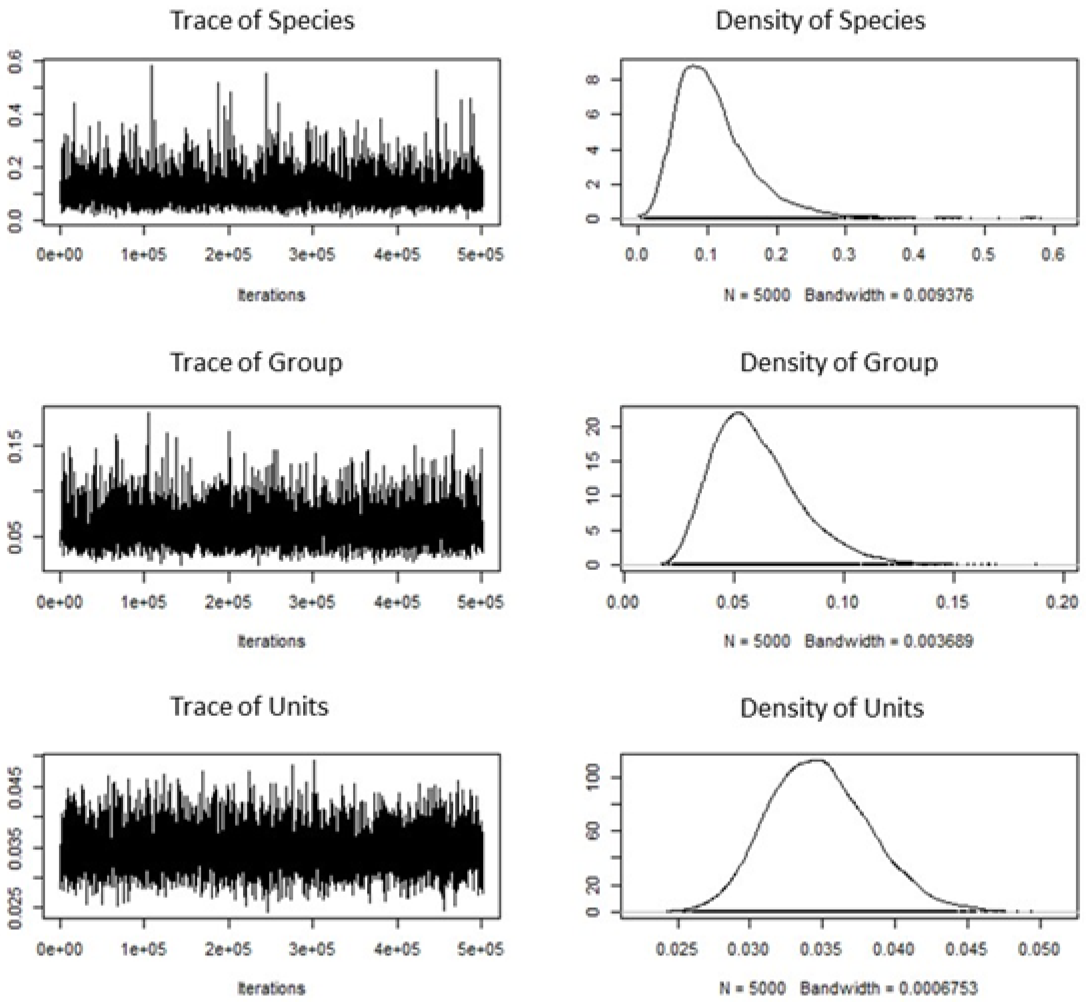











Trace of Species
0.0
0.2
0.4
0.6
0e+00
1e+05
2e+05
3e+05
4e+05
5e+05
Iterations
Density of Species
0
2
4
6
8
0.0
0.1
0.2
0.3
0.4
0.5
0.6
N = 5000 Bandwidth = 0.009376
Trace of Group
0.05
0.15
0e+00
1e+05
2e+05
3e+05
4e+05
5e+05
Iterations
Density of Group
0
5
10
15
20
0.00
0.05
0.10
0.15
0.20
N = 5000 Bandwidth = 0.003689
Trace of Units
0.025
0.035
0.045
0e+00
1e+05
2e+05
3e+05
4e+05
5e+05
Iterations
Density of Units
0
20
60
100
0.025
0.030
0.035
0.040
0.045
0.050
N = 5000 Bandwidth = 0.0006753

Appendix 7 - Additional results

We report here additional results to demonstrate the robustness of our finding that given tolerance (measured by aggression DII) is positively related to vocal rate to alternative model specifications.

1. Individual-level analysis: Vocal rate is positively associated with Given tolerance measure ‘Aggression DII’. The model in the main manuscript used a Gaussian distribution using log10 transformation on the dependent variable. Table A provides the results of the same model but with Poisson distribution using untransformed vocal rate rounded to the nearest integer as the dependent variable. Table B provides the results for a Gaussian model using the raw, untransformed dependent variable. All models included the same four given tolerance measures (Aggression DII, Intensity, Counteraggression and Grooming DII) and group size as fixed effects, while group and species identities are included as random effects. All models confirm that aggression DII is positively associated with vocal rate.

Table A

Results of MCMC model with Given Tolerance measures as fixed effects (N individuals=162, N groups = 41, N species = 14) using a Poisson Distribution (dependent variable rounded). Fixed effects explain 6% of variance, while random effects of group and species explain 32% and 56%, respectively.

Fixed Effect	**Posterior Mean β**	**1-95% CI**	**u-95% CI**	**pMCMC**
Aggression DII	1.05	.09	2.01	.03
Groom DII	-.39	-1.23	.49	.37
Counter-aggression	-.50	-1.94	.89	.49

Aggression Intensity	-.08	-.71	.53	.81
Group Size	.005	-.03	.04	.77

Table B

Results of MCMC model with Given Tolerance measures as fixed effects (N individuals=162, N groups = 41, N species = 14) using a Gaussian distribution with no transformation on the dependent variable. Fixed effects explain 7% of variance, while random effects of group and species explain 27% and 34% respectively.

Fixed Effect	**Posterior Mean β**	**1-95% CI**	**u-95% CI**	**pMCMC**
Aggression DII	7.16	2.01	12.81	.01
Groom DII	-2.41	-6.78	2.07	.28
Counter-aggression	-4.47	-12.90	3.96	.29
Aggression Intensity	-.65	-3.69	2.47	.68
Group Size	-.01	-.11	.09	.87

2. Individual-level analysis: Vocal rate is positively associated with Given tolerance measure ‘Aggression DII’. The model in the main manuscript used all four given tolerance measures as fixed effects, and required any individuals with missing data for any of these measures to be excluded. This resulted in the exclusion of 91 individuals and five species with aggression symmetry data. To check whether the relationship between aggression symmetry (given tolerance form) and vocal rate

generalises across all individuals with aggression symmetry data, we ran a model excluding all other given tolerance measures as fixed effects, thus including all individuals and species with aggression symmetry data. We used a Gaussian distribution with a log10 transformation on the dependent variable, and again confirmed that aggression symmetry is positively related to vocal rate. Table C shows the results from the model.

Table C

Results of MCMC model with group size and given tolerance measure of Aggression DII as fixed effects (N individuals =253, N groups = 54, N species=19) using a Gaussian distribution with log10 transformation on the dependent variable. Fixed effects explain 3% of variance, while random effects of group and species explain 29% and 50%, respectively.

Fixed Effect	**Posterior Mean β**	**1-95% CI**	**u-95% CI**	**pMCMC**
Aggression DII	.20	-.01	.40	.06
Group Size	-.001	-.009	.006	.77

Appendix 8 – Species, groups and individuals included in models

The data included in the paper are a mixture of data collected specifically for the current project and those collected for previous unrelated projects. We also applied minimum criteria for all of our measures. For this reason we do not have data from all individuals, groups or species for all measures, and thus not all are included in our models. Tables A – F indicate the species and number of groups in each species that were included in our models.

Table A

Given Tolerance full model i): Species, groups and individuals included in the GLMM with vocal rate as the dependent variable, group and species as random effects, and group size and the four given tolerance measures as fixed effects

Species	Common Name	N groups	N individuals
Macaca assamensis	Assamese Macaques	1	14
Macaca sylvanus	Barbary Macaques	2	10
Alouatta pigra	Black Howler Monkeys	1	2
Macaca radiata	Bonnet Macaques	3	20
Pan troglodytes schweinfurthii	Chimpanzees	2	22
Macaca nigra	Crested Macaques	2	15
Theropithecus gelada	Geladas	9	17
Indri indri	Indris	2	2
Macaca fuscata	Japanese Macaques	1	5
Gorilla beringei	Mountain gorillas	1	4
Papio anubis	Olive Baboons	2	22
Ateles geoffroyi	Spider Monkeys	1	3
Propithecus verreauxi	Verreaux's Sifaka	13	25
Chlorocebus pygerythrus	Vervet Monkeys	1	1

Table B

Given Tolerance Aggression DII model: Species, groups and individuals included in the GLMM with vocal rate as the dependent variable, group and species as random effects, and group size and given tolerance form of aggression DII as fixed effects

Species	**Common Name**	**N groups**	**N individuals**
Macaca assamensis	Assamese Macaques	1	16
Macaca sylvanus	Barbary Macaques	2	13
Alouatta pigra	Black Howler Monkeys	2	3
Macaca radiata	Bonnet Macaques	3	24
Pan paniscus	Bonobos	1	9
Pan troglodytes schweinfurthii	Chimpanzees	2	24
Macaca nigra	Crested Macaques	2	16
Theropithecus gelada	Geladas	13	30
Indri indri	Indris	2	4
Macaca fuscata	Japanese Macaques	1	5
Papio kindae	Kinda Baboons	1	3
Gorilla beringei	Mountain gorillas	1	5
Papio anubis	Olive Baboons	2	38
Cercopithecus ascanius	Red Tailed Monkeys	2	6
Cercocebus torquatus atys	Sooty Mangabeys	1	17
Ateles geoffroyi	Spider Monkeys	2	5
Propithecus verreauxi	Verreaux’s Sifaka	13	30
Chlorocebus pygerythrus	Vervet Monkeys	1	1

Gorilla gorilla gorilla	Western Gorillas	1	4

Table C

Received Tolerance full model ii): Species, groups and individuals included in the GLMM with vocal rate as the dependent variable, group and species as random effects, and group size and the four received tolerance measures as fixed effects

Species	**Common Name**	**N groups**	**N individuals**
Macaca assamensis	Assamese Macaques	1	12
Macaca sylvanus	Barbary Macaques	2	6
Macaca radiata	Bonnet Macaques	3	14
Pan troglodytes schweinfurthii	Chimpanzees	2	23
Macaca nigra	Crested Macaques	2	13
Theropithecus gelada	Geladas	8	19
Indri indri	Indris	2	2
Macaca fuscata	Japanese Macaques	1	2
Gorilla beringei	Mountain gorillas	1	5
Papio anubis	Olive Baboons	2	24
Ateles geoffroyi	Spider Monkeys	1	3
Propithecus verreauxi	Verreaux's Sifaka	13	24

Table D

Feeding Proximity model iii): Species, groups and individuals included in the GLMM with vocal rate as the dependent variable, group and species as random effects, and group size and feeding proximity as fixed effects

Species	**Common Name**	**N groups**	**N individuals**
Pan paniscus	Bonobos	1	19
Pan troglodytes schweinfurthii	Chimpanzees	1	7
Macaca nigra	Crested Macaques	2	19
Theropithecus gelada	Geladas	21	116
Indri indri	Indris	7	19
Cercopithecus ascanius	Red Tailed Monkeys	2	15
Cercocebus torquatus atys	Sooty Mangabeys	1	24
Chlorocebus pygerythrus	Vervet Monkeys	1	13

Table E

Main species level repertoire models iv),vi),vii): Species and groups included in the three main PGLS models with one of the three repertoire measures as the dependent variable, and group size and dominance style composite index as the predictor variables, with lambda set to 1.

Species	**Common Name**	**N Groups**
Macaca assamensis	Assamese Macaques	1
Macaca sylvanus	Barbary Macaques	2
Alouatta pigra	Black Howler Monkeys	3
Macaca radiata	Bonnet Macaques	3
Pan paniscus	Bonobos	1

Pan troglodytes schweinfurthii	Chimpanzees	2
Macaca nigra	Crested Macaques	2
Theropithecus gelada	Geladas	37
Ateles geoffroyi	Geoffroy's spider monkeys	2
Indri indri	Indris	7
Macaca fuscata	Japanese Macaques	3
Gorilla beringei	Mountain Gorillas	1
Papio anubis	Olive Baboons	3
Eulemur rufifrons	Red fronted lemurs	4
Cercopithecus ascanius	Red tailed Monkeys	2
Lemur catta	Ring Tailed Lemurs	5
Cercocebus torquatus atys	Sooty Mangabeys	1
Chlorocebus pygerythrus	Vervet Monkeys	3
Gorilla gorilla gorilla	Western Gorillas	1
Papio cynocephalus	Yellow Baboons	5

Table F

Counteraggression species level models: Species and groups included in the PGLS model with N of hierarchy-related calls as the dependent variable, and counteraggression as the predictor variable (PGLS model also has lambda set to 1)

Species	**Common Name**	**N Groups**
Macaca assamensis	Assamese Macaques	1
Macaca sylvanus	Barbary Macaques	1
Alouatta pigra	Black Howler Monkeys	1
Macaca radiata	Bonnet Macaques	3
Pan paniscus	Bonobos	1
Pan troglodytes schweinfurthii	Chimpanzees	1
Macaca nigra	Crested Macaques	2
Theropithecus gelada	Geladas	5
Ateles geoffroyi	Geoffroy's spider monkey	2

Indri indri	Indris	3
Macaca fuscata	Japanese Macaques	2
Gorilla beringei	Mountain Gorillas	1
Papio anubis	Olive Baboons	2
Eulemur rufifrons	Red fronted lemurs	3
Chlorocebus pygerythrus	Vervet Monkeys	1

Appendix 9 – Group size and repertoire size graph

The figure below indicates the relationship between group size and repertoire size from our sample, which shows a slightly negative relationship.

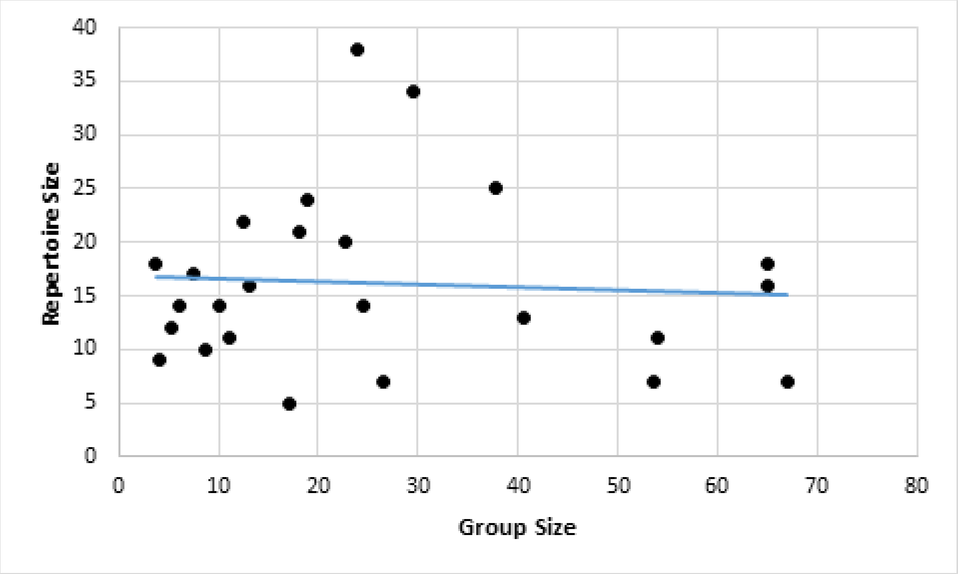


Figure A Relationship between group size (listed in table 3 of main text) and repertoire size (listed in S8 table A) from the 26 species in our sample. The trend line shows a slightly negative relationship.

Chapter 3

Appendix 10 – Subject details

Table A

Sex, dates of birth, sub-species (for chimpanzees) and rearing history of all subjects in the sample.

Species	Group	Name	Sex	Date of Birth	Sub-species
Chimpanzees	Edinburgh	Cindy	Female	01/01/1964	*P.t.troglodytes*
		Edith	Female	11/04/1996	Hybrid
		Emma	Female	15/08/1981	*P.t.troglodytes*
		Eva	Female	09/12/1980	Hybrid
		Heleen	Female	16/04/1991	*P.t.verus*
		Kilimi	Female	20/02/1993	Hybrid
		Lianne	Female	14/02/1989	*P.t.verus*
		Lucy	Female	11/11/1976	Hybrid
		Pearl	Female	01/01/1969	*P.t.verus*
		Sofie	Female	22/11/1981	*P.t.verus*
		David	Male	02/02/1975	Hybrid
		Frek	Male	21/10/1993	*P.t.verus*
		Kindia	Male	05/02/1997	Hybrid
		Liberius	Male	20/01/1999	Hybrid
		Louis	Male	01/01/1976	*P.t.verus*
		Paul	Male	08/05/1993	*P.t.verus*
		Qafzeh	Male	31/03/1992	Hybrid
		Rene	Male	21/02/1993	*P.t.verus*
	Leipzig (Group A)	Kisha	Female	03/04/04	*P.t.verus*

	Tai	Female	12/08/02	Hybrid
	Swela	Female	10/19/95	*P.t.verus*
	Natasha	Female	03/28/80	*P.t.verus*
	Riet	Female	11/11/77	Hybrid
	Maja	Female	05/01/86	Hybrid
	Fraukje	Female	04/06/76	*P.t.verus*
	Corry	Female	12/12/76	*P.t.verus*
	Bambari	Female	12/08/2000	Hybrid
	Dorien	Female	10/22/80	*P.t.verus*
	Sandra	Female	06/09/93	Hybrid
	Lome	Male	11/08/01	*P.t.verus*
	Lobo	Male	21/04/04	*P.t.verus*
	Frodo	Male	11/28/93	*P.t.verus*
	Bangolo	Male	07/05/09	*P.t.verus*
	Kofi	Male	07/07/05	*P.t.verus*
	Robert	Male	12/01/75	*P.t.verus*
Leipzig (Group B)	Jeudi	Female	1966	*P.t.schweinfurthii*
	Frederike	Female	1974	*P.t.schweinfurthiii*
	Daza	Female	1986	*P.t.verus*
	Hope	Female	12/14/90	Hybrid
	Zira	Female	06/03/97	Hybrid
	Alex	Male	03/10/01	Hybrid
Vallée des Singes	Panya	Female	14/07/2008	*P.t.verus*
	Lila	Female	20/06/2009	*P.t.verus*
	Cauna	Female	05/05/2007	*P.t.verus*
	Jorg	Male	01/01/1995	*P.t.verus*
	Conan	Male	20/03/1996	*P.t.verus*

	Wonder	Male	19/03/1997	*P.t.verus*
Kanyawara	Omusisa	Female	23/06/2005	*P.t.schweinfurthii*
	Likizo	Male	29/12/2004	*P.t.schweinfurthii*
	Fisher	Female	02/07/2004	*P.t.schweinfurthii*
	Tsunami	Female	23/01/2005	*P.t.schweinfurthii*
	Unasema	Male	02/11/2004	*P.t.schweinfurthii*
	Bono	Male	08/10/2003	*P.t.schweinfurthii*
	Delta	Female	02/07/2003	*P.t.schweinfurthii*
	Jumbo	Female	02/07/2003	*P.t.schweinfurthii*
	Gaga	Female	02/07/2002	*P.t.schweinfurthii*
	Tacugama	Male	05/04/2001	*P.t.schweinfurthii*
	Special	Female	09/02/2000	*P.t.schweinfurthii*
	Tuber	Male	03/11/2000	*P.t.schweinfurthii*
	Tuke	Male	02/11/1999	*P.t.schweinfurthii*
	Alison	Female	01/01/2000	*P.t.schweinfurthii*
	Tripoli	Female	02/07/1999	*P.t.schweinfurthii*
	Leona	Female	02/07/1997	*P.t.schweinfurthii*
	Michelle	Female	02/07/1997	*P.t.schweinfurthii*
	Max	Male	15/01/1998	*P.t.schweinfurthii*
	Rwanda	Female	02/07/1996	*P.t.schweinfurthii*
	Lanjo	Male	13/08/1995	*P.t.schweinfurthii*
	Eslom	Male	02/07/1994	*P.t.schweinfurthii*
	Bud	Male	20/01/1995	*P.t.schweinfurthii*
	Quinto	Female	02/07/1992	*P.t.schweinfurthii*
	Wilma	Female	02/07/1992	*P.t.schweinfurthii*
	Zaire	Female	02/07/1992	*P.t.schweinfurthii*
	Wangari	Female	02/07/1991	*P.t.schweinfurthii*
	Zanzibar	Female	02/07/1986	*P.t.schweinfurthii*
	Lia	Female	02/07/1982	*P.t.schweinfurthii*

		Makoku	Male	02/07/1982	*P.t.schweinfurthii*
		Umbrella	Female	02/07/1981	*P.t.schweinfurthii*
		Tongo	Female	02/07/1980	*P.t.schweinfurthii*
		Outamba	Female	02/07/1979	*P.t.schweinfurthii*
		Johnny	Male	02/07/1974	*P.t.schweinfurthii*
		Yogi	Male	02/07/1973	*P.t.schweinfurthii*
		Zimbabwe	Female	02/07/1971	*P.t.schweinfurthii*
		Mususu	Female	02/07/1970	*P.t.schweinfurthii*
		Big Brown	Male	02/07/1966	*P.t.schweinfurthii*
		Bubbles	Female	02/07/1960	*P.t.schweinfurthii*
Bonobos	San Diego	Lisa	Female	14/06/1991	NA
		Kallie	Female	15/03/2005	NA
		Loretta	Female	22/01/1974	NA
		Mali	Female	09/04/2007	NA
		Maddie	Female	24/03/2009	NA
		Vic	Male	27/06/2001	NA
		Erin	Male	23/12/1991	NA
		Makasi	Male	22/04/2004	NA
	Leipzig	Joey	Male	12/13/82	NA
		Jasongo	Male	08/02/90	NA
		Kuno	Male	11/26/1996	NA
		Gemena	Female	11/07/2005	NA
		Fimi	Female	07/28/08	NA
		Luiza	Female	27/01/05	NA
		Lexi	Female	09/13/99	NA
		Yasa	Female	08/27/97	NA

Vallée des Singes (Group A)				
	Daniela	Female	17/06/1968	NA
	Khaya	Female	19/10/2001	NA
	Lingala	Female	17/07/2003	NA
	Ukela	Female	19/12/1985	NA
	Lucy	Female	01/12/2003	NA
	Khalessi	Female	12/12/2012	NA
	Ulindi	Female	10/10/1993	NA
	Yahimba	Female	07/08/2009	NA
	Diwani	Male	11/08/1996	NA
	David	Male	27/07/2001	NA
	Kelele	Male	22/07/2004	NA
	Moko	Male	04/08/2012	NA
	Loto	Male	02/09/2009	NA
Vallée des Singes (Group A)				
	Lisala	Female	24/04/1980	NA
	Lingoye	Female	29/11/2007	NA
	Kutu	Female	29/05/1998	NA
	Omanga	Female	18/12/2008	NA
	Bondo	Male	17/09/1991	NA
	Luebo	Male	18/03/2006	NA
Lui Kotale	Gwen	Female	~18-21	NA
	Iris	Female	>28	NA
	Luna	Female	~14-16	NA
	Martha	Female	>33	NA
	Nina	Female	~14-16	NA

Olga	Female	>28	NA
Paula	Female	>28	NA
Rio	Female	>28	NA
Susie	Female	~18-21	NA
Uma	Female	~18-21	NA
Wilma	Female	~14-16	NA
Zoe	Female	>28	NA
Apollo	Male	~15-20	NA
Ben	Male	~20-30	NA
Camillo	Male	~30-40	NA
Emile	Male	~15-20	NA
Jack	Male	~20-30	NA
Roque	Male	~10-15	NA
Zed	Male	~10-15	NA

Note: P.t.=Pan troglodytes

Appendix 11 - Ethics

The table below provides details of ethics approval from the six data collection locations.

Table A

Ethics details for all fieldsites in sample.

Location	**Ethics Details**
Leipzig Zoo	This study complied with the ASAB/ABS guidelines for the use of animals in research and was granted ethical approval by theBiology Animal Welfare Ethical Review Board (AWERB), University of York. All data collection was approved by the zookeepers in charge of the apes.
Vallée des Singes	This study complied with the ASAB/ABS guidelines for the use of animals in research and was granted ethical approval by the Biology Animal Welfare Ethical Review Board (AWERB), University of York. All data collection was approved by the zookeepers in charge of the apes.
San Diego Zoo	Data collection received ethical approval from the IACUC committee of San Diego Zoo Global (Project number #17-007)
Edinburgh Zoo	Ethical approval for long term observational data collection in Budongo Trail was obtained from the Biology Animal Welfare Ethical Review Board (AWERB), University of York.
Kanyawara	Permissions to conduct this study were granted by the Ugandan Wildlife Authority and the Ugandan National Council of Science and Technology
LuiKotale	Research permit was granted by the Institut Congolais pour la Conservation de la Nature (MIN.0242/ICCN/DG/GMA/013/2013)

Appendix 12 – Sampling effort

Table 1

N of individuals included in all measures and reasons for missing data

		Overall												**Same-Sex: Males**			**Same-Sex: Females**		
		Aggression Intensity	**Counteraggression**	**Rate low intensity aggression**	**Aggression DII**	**Groom DII**	**Reconciliation**	**Feeding Proximity**	**Grooming Rate**	**Non-feeding Proximity**	**Chimpanzee Dominance Style Component Score**	**Bonobo Component 2 score**	**Bonobo Component 3 score**	**Chimpanzee Dominance Style Component Score**	**Bonobo Component 2 score**	**Bonobo Component 3 score**	**Chimpanzee Dominance Style Component Score**	**Bonobo Component 2 score**	**Bonobo Component 3 score**
Chimpanzees	Edinburgh	12	A	B	18	18	A	18	B	18	18	C	C	8	C	C	D	C	C
	Leipzig (Group A)	15	15	17	17	17	14	17	17	17	17	C	C	6	C	C	11	C	C
	Leipzig (Group B)	2	2	6	3	6	NA	6	6	6	6	C	C	D	C	C	5	C	C
	Vallée des Singes	7	7	7	7	7	7	7	7	7	7	C	C	4	C	C	3	C	C
	Kanyawara	26	26	29	28	29	NA	26	29	26	29	C	C	14	C	C	15	C	C
Bonobos	San Diego	6	6	8	7	8	A	8	8	8	C	8	7	C	2	3	C	4	5
	Leipzig	6	6	8	7	8	7	8	8	8	C	8	7	C	1	3	C	5	5
	Vallée des Singes (Group A)	12	12	13	12	13	12	13	13	13	C	13	13	C	5	5	C	8	8
	Vallée des Singes (Group B)	5	5	6	6	6	6	6	6	6	C	6	6	C	2	2	C	2	4
	LuiKotale	18	A	B	18	17	A	19	19	19	C	18	18	C	7	6	C	9	9

*Note:*A= Data not collected during observation period
B= Bout definition could not be made consistent with other groups
C= Measure does not apply to species
D= Insufficient data available to meet minimum criteria for inclusion

Chapter 4

Appendix 13 – Modality Availability

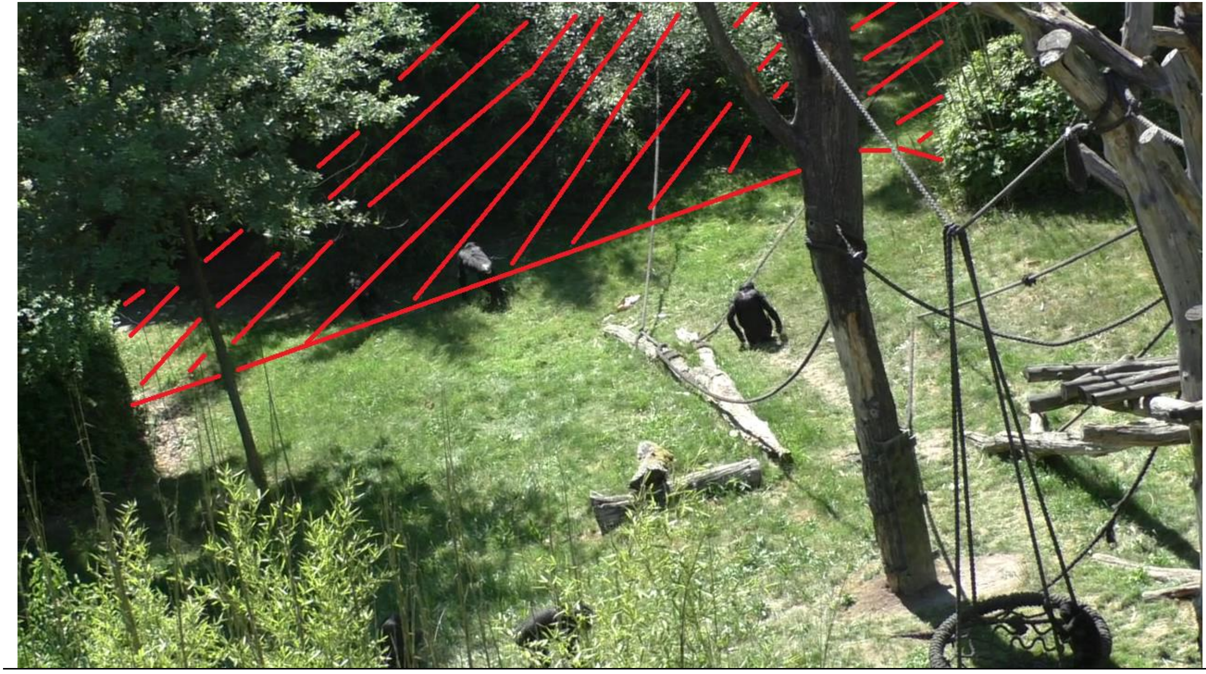
Table A provides definitions for modality availability as used in the communication coding scheme on Observer X.

Table A

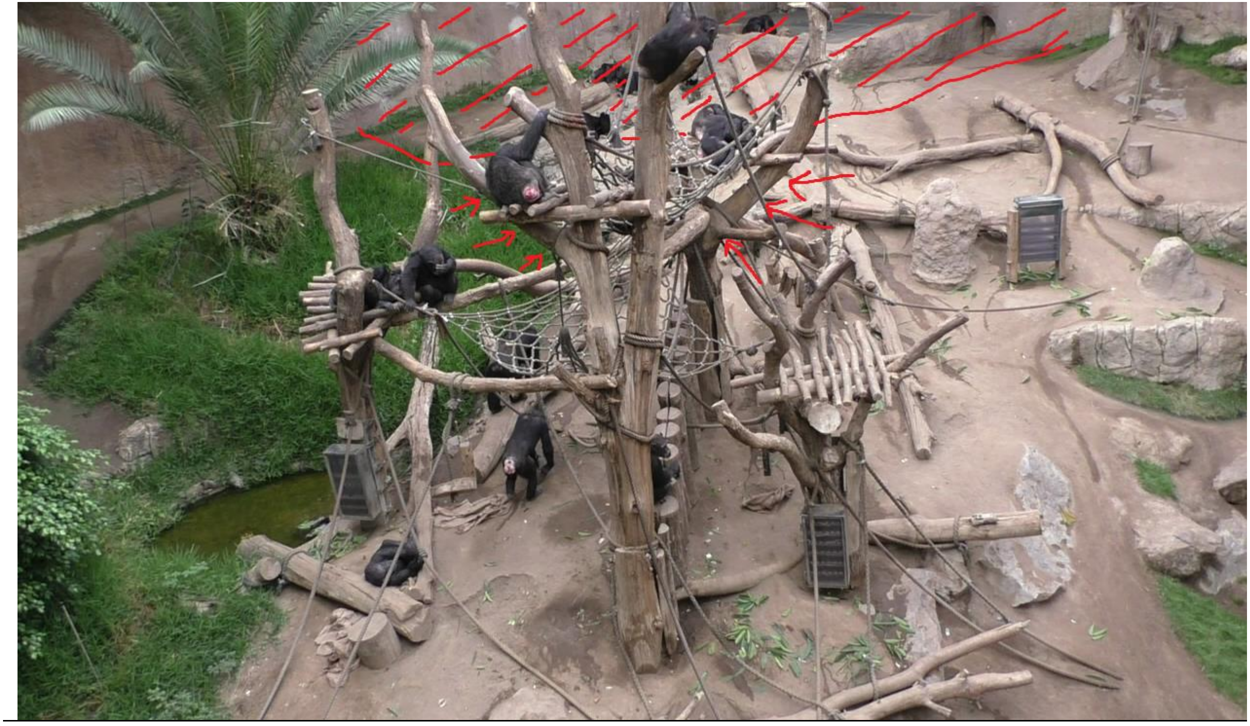
Definitions of Modalities available from communication coding scheme instructions.

Modality Available	Description
Vocalisations	Available if exact location of the focal subject is known, is not in the red highlighted sections of the images below (as they are determined too far away from observation point or too noisy an area), and if a vocalisation was produced, it would be possible to identify whether or not it was produced by the focal. Unavailable when, if a vocalisation was heard, it would not be possible to identify whether or not it was produced by the focal. Egs., • the individual is in close proximity (within arms reach) to other individuals and their faces aren't visible, so discriminating which individual vocalised would be very difficult. (If faces of all other individuals can be seen, it can be coded as available, as if a vocalisation occurred it would be clear who it was). • If the focal's face can't be seen, and there is a lot of noise (ie., others vocalising).

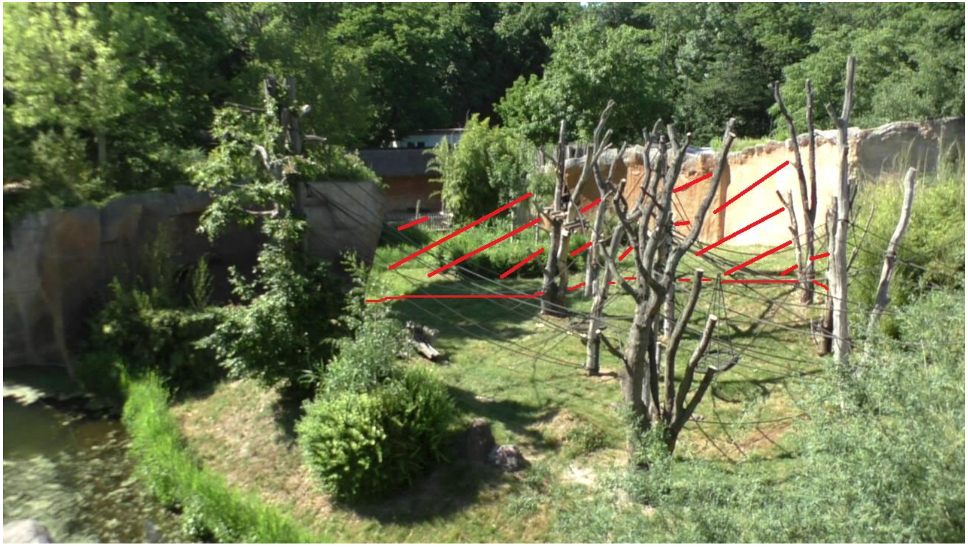
Leipzig Bonobos:



Leipzig A Chimps



Leipzig B Chimps



Facial expressions	Available if the face can be seen from the front or side, or from any other angle that still allows sufficient sight of the mouth and eyes. Coded as unavailable when the mouth region cannot be seen at all.
Gestures	Available if majority of torso and arms are visible. Coded as unavailable when neither arm is visible.

Appendix 14 – Communicative Repertoires

Tables A, B, C and D below outline the communicative repertoires for gestures, facial expression, chimpanzee vocalisations and bonobo vocalisations, respectively.

Table A

Gestural Repertoire for chimpanzees and bonobos, from Graham & Byrne (2016); Hobaiter & Byrne (2011)

Gesture	**Description of gesture types**
Arm raise	Raise arm(s) and/or hand(s) vertically in the air
Arm shake	Small repeated back and forth motion of the arm
Arm swing	Large back and forth movement of the arm(s) held below the shoulder
Arm up	Extend straight arm(s) out to side and away from body
Arm wave	Large repeated back and forth movement of the arm(s) raised above the shoulder
Beckon	Hand is moved in an upwards sweep from the elbow or wrist towards the signaller
Big loud scratch	Loud exaggerated scratching movement on the signaller’s own body
Bipedal rocking	Stand or walk bipedal, rock forward and back or side to side, repeated (includes rare ‘Quadrupedal rocking’)
Bipedal stance	Stand bipedal, arms out to side, back arched
Bite	Recipient’s body is held between the teeth of the signaller
Bounce	Standing quadrupedal, bend elbows and knees to move up and down repeatedly
Bow	Signaller bends forward from the waist while standing [bipedal]
Dangle	To hang from one or both arms from a branch above another individual; this is audible as there is normally significant disturbance of the canopy
Directed push	A light short non-effective push that indicates a direction of desired movement, immediately followed by the recipient moving as indicated
Embrace	Signaller wraps [one or] both arms around the recipient and maintains physical contact
Foot dangle	Repeated back and forth movement of feet from the ankles
Foot present	Sole of the foot is presented to the recipient

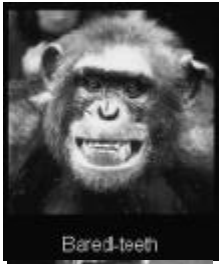
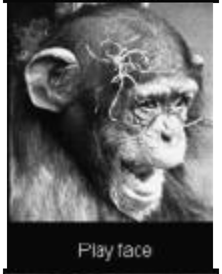
Gallop	An exaggerated running movement where the contact of the hands and feet is deliberately audible
Grab	The hand[(s)] is[/are] firmly closed over part of the recipient’s body
Grab-pull	As ‘Grab’ but closed hand contact is maintained and a force exerted to move the recipient from their current position
Hand fling	Rapid movement of the hand or arm in the direction of the recipient Includes Swat - NEW: Swipe hand in sharp downward motion without making contact with the recipient
Hand on	Palm[(s)] of the hand[(s)] is[/are] placed on the recipient, contact lasts for more than 2 s
Hand shake	Repeated back and forth movement of hand from the wrist
Head butt	Head is briefly and firmly pushed into the body of the recipient
Head rock	Repeated back and forth [or side to side] movement of the head (includes ‘Head shake’)[4]
Head stand	Signaller bends forward and places head on the ground
Hip thrust	Sitting, crouching, or standing, thrust hips forward (single or repeated)
Hit with object	An object is brought into short, hard contact with the body of the recipient
Jump	While bipedal, both feet leave the ground simultaneously, accompanied by horizontal displacement through the air
Kick	Foot is brought into short hard contact with the recipient’s body in a movement from the hip with a horizontal element (for vertical see ‘Stomp other’)
Knock object	Back of the hand or knuckles are brought into short, hard, audible contact with an object
Leaf drop	Pick leaf(s) and drop it, usually signaller is above recipient
Leg flap	Sitting with knees bent, open and close one or both legs to side (single or repeated)
Leg swing	Large back and forth movement of the leg from the hip
(Look[5])	Signaller holds an eye-contact position with the recipient–minimum duration 2 s
Mouth stroke	Signaller’s palm and fingers are repeatedly run over the mouth area of the recipient
Object move	Object is displaced in one direction, contact is maintained through movement (includes ‘Branch drag’)

Object shake	Repeated back and forth movement of an object (includes ‘Object shake tandem’) Object shake tandem: As ‘Object shake’ but object is in contact with the recipient
Pirouette	Signaller turns around their body’s vertical axis while also displacing along the ground
Poke	Firm, brief push of one or more fingers into the recipient’s body
Pounce	Signaller displaces through the air to land quadrupedally on the body of the recipient
Present (climb on)	Arm or leg is extended to young recipient in order to facilitate them climbing onto the signaller’s body (normally mother to infant)
Present (grooming)	Body is moved to deliberately expose an area to the recipient’s attention which is immediately followed by grooming of the area
Present	Signaller approaches recipient backwards, exposing the swelling or anus to the recipient’s face Present genitals forwards: the signaller sits and spreads their limbs displaying their genital swelling or erect penis
Punch other	As ‘Punch object/ground’ but contact is with recipient’s body
Push	Palm in contact with recipient’s body and force is exerted in an attempt to displace recipient
Reach	Arm extended to the recipient with hand in an open, palm upwards[, downwards, or sideways] position (modified from Hobaiter & Byrne 2011 to include ‘Reach – palm down’, ‘Reach – palm side’, ‘Reach – palm up’, and ‘Reach – wrist first’)
Rocking	Sitting, rock forward and back or side to side, repeated
Roll over	The signaller rolls onto their back exposing their stomach, normally accompanied by repeated movements of the arms and/or legs
Rump rub	Push/rub rump against the body/swelling of recipient
Shake hands	Signaller grasps recipient’s hand in their own hand and then makes small repeated back and forth movements from the wrist
Side roulade	Body is rotated around the head-feet axis while lying on the ground with horizontal displacement along the ground
Slap object/ground	Movement of the arm from the shoulder with hard, short contact of the palm of the hand to an object [or the ground]
Slap object/ground with object	As ‘Slap object’ but the hand holds an object which is brought into contact with another object [or the ground] (e.g. a branch is slapped against a tree)
Slap other	As ‘Slap object’ but the palm is brought into contact with the recipient’s body

Somersault	Signaller's body is curled into a compact position on the ground, and rolled forwards so the feet are brought over the head and returned to a sitting position
Stiff walk	Walk quadrupedally with a slow, exaggerated movement
Stomp	Sole of the foot is lifted vertically and brought into a short, hard, audible contact with the surface being stood upon (e.g. ground or a branch)
Stomp other	As 'Stomp' but contact is made with recipient
Stomp 2-feet	As 'Stomp' but both feet used, normally alternately
Stomp 2-feet other	As 'Stomp 2-feet' but contact is made with the recipient
Stroking	Run palm of hand gently over recipient's body repeatedly (in Hobaiter & Byrne 2011, 'Stroking' was included in 'Touch other')
Tandem walk	[Signaller] positions arm over the body of the recipient and both walk forward while maintaining position
Tap object	Movement of the arm from the wrist of elbow, with firm, short contact of the fingers to the object (single/multiple)
Tap other	As Tap object' but contact is with the recipient's body
Throw object	Object is moved and released so that there is displacement through the air after moment of release
Touch/Knock other	Light contact with the palm and/or fingers on the body of the recipient, contact under 2 s
Water splash	Hand is moved vigorously through the water so that there is audible displacement of the water

Table B

Facial Expression Repertoire for chimpanzees and bonobos. All images are taken from Parr, Waller, Vick & Bard (2007) and Parr & Waller (2006).

Facial Expression	Description
Bared teeth display	
Play face	
Pant hoot face	
Scream face	
Alert face	
Pout	

Whimper face

Table C

Vocal Repertoire for chimpanzees, taken from Slocombe & Zuberbuehler (2010).

Vocalisation	Description
Pant hoot	Species-typical long-distance vocalisation with four distinct phases: introductory phase (low frequency hoo calls), buildup phase (increasingly loud panted hoo calls with energy in both the inhalation and exhalation), climax phase (screams or roars), and letdown phase (resembles the buildup phase but with progressively decreasing energy). Calls often do not include all four phases; introduction and let-down are commonly omitted.
Pant grunt	Noisy, low-frequency grunts or barks, panted in a rapid rhythm with audible energy in both inhalation and exhalation.
Scream	Loud, high-pitched, harmonic vocalisation with varying degrees of tonality. They are almost always given in bouts, but the length of a bout can vary from a few seconds to several minutes. In most contexts acoustic energy is present only during exhalation, but during intense tantrums it is often present during inhalation as well.
Bark	Sharp, loud calls with abrupt onsets. They are often noisy and are generally low-pitched vocalisations.
Waa bark	A distinct loud, intimidating bark variant in which the sound “waa” is clear. Acoustically distinct from the shorter barks and screams into which they often grade, waa-barks typically have a low frequency “w” introduction at call onset, and then clear rise and short fall in pitch during the “aa” element of the call. Waa-barks are produced in isolation of in short series.
Pant	Unvoiced, soft, low-frequency sounds. Temporal patterning is regular and rapid.
Grunt	Short, soft low-frequency calls given singularly or in short bouts.
Rough grunt	An umbrella term that describes the vocalisations produced by individuals when approaching, collecting, or consuming food. Acoustically, rough grunts grade from low-frequency, unvoiced, noisy grunts to high-frequency tonal squeaks.
Cough	Low-frequency vocalisation, similar to a grunt but rarely voiced. A short noisy signal with no harmonic structure.
Laughter	Noisy, low-frequency grunts and moans delivered in an irregular rhythm, reminiscent of hoarse, wheezing human laughter. Acoustic energy is audibly present in both inhalation and exhalation, with most voicing occurring during inhalation.
Whimper	A series of soft low-frequency hoo calls that can become higher in both frequency and amplitude as a bout progresses. The frequency and amplitude often rises and falls throughout a bout.

	Individual hoo calls are tonal signals with a variable number of harmonics.
Squeak	High-pitched, short calls often given in fast succession to form short bouts. The calls are tonal signals, often with clear harmonic structure.
Other vocalisation	Focal produces a vocalisation not listed above. Must be described in the notes next to this coded signal.

Table D

Vocal Repertoire for bonobos, taken from de Waal (1988).

Vocalisation	Description
Low Hoot	This is the species' lowest-pitched vocalization, uttered in series in which both inspirations and expirations are vocalized. Spectral energy is concentrated in two unmodulated bands: the lower one band is approximately 500 Hz, The rhythm is in the order of 3-4 sounds per second. The vocalization may but need not develop into 'high hooting' . Often a couple of high hoots are given interspersed with the low hoots before the display ends. Transitions between low and high hooting are abrupt and may go back and forth. The facial expression is one with pouted lips.
High Hooting	Two types of high-pitched long-distance whooping calls can be distinguished. Staccato hooting consists of brief, sharp calls which reach an average peak frequency of 2.3 kHz in the lowest harmonic. This peak occurs in the middle, or slightly before the middle of the call, which lasts an average of 0.15 sec. At close range, the sounds are earpiercingly shrill and explosive; at a distance, they sound like the yapping of a small dog. During choruses, staccato hooting of different individuals is almost perfectly synchronized so that one individual acts as the "echo" of another, or emits calls at the same moments as another. The calls are given in a steady rhythm of about two per second. The second vocalization, called legato hooting, reaches the same peak frequency of 2.3 kHz in the lowest harmonic but continues with a relatively long, modulated second section. As a consequence the peak frequency occurs far before the middle of the call, and the vocalization has a less sharp, more melodious quality. The average duration is 0.30 sec, but legato hoots of up to 0.70 sec have been recorded. Legato hooting, too, occurs in series, but both the duration per call and the rhythm of emission are irregular. At the very beginning of every legato hoot a low-frequency harmonic is distinguishable in the spectrogram with a starting frequency at approximately the level of the lowest harmonic in 'low hooting'. This brief build-up occurs independently of whether the vocalization was actually preceded by low hooting or not. As a result, one can hear a hollow-sounding onset before a legato hoot reaches its full strength and pitch. Such build-up sounds are absent in staccato hooting. Although the two types of high hooting can be distinguished by ear, I did not start doing so till half-way through my study. Moreover, since 1) transitions between the two types occur

	regularly, and 2) both types can be heard simultaneously during choruses, there may exist enough similarity in causation and function to take them together. Typically, during high hooting the mouth is opened with the lips slightly pouted, covering the teeth. Lip retraction resulting in teeth-baring does occur, however.
Wieew-Bark	A single, very loud bark in which one can hear the voice rise and fall. The "wieew"-bark is clearly related to 'legato hooting'. It builds up with the same low-pitched harmonic and reaches the same peak frequency of approximately 2.3 kHz in the lowest harmonic. Instead of occurring at the beginning of the call, however, the peak falls just before the middle, A second section is lacking, and the call never reaches the duration of some of the legato hoots, the average duration being 0.25 sec. If one individual utters several "wieew"-barks the intervals between them are irregular and over one second long, each call being a separate utterance. The facial expression is as described for high hooting with the mouth more wide
Contest Hooting	A relatively unmodulated pure call with a peak of about 2.3 kHz in the lower harmonic and an average duration of 0.15 sec. This vocalization belongs to the hooting and "wieew"-bark complex. Contest hooting is softer, tonally flatter, and monosyllabic, but does reach the same pitch and sounds like a restrained form of 'legato hooting'. Contest hooting series have a rhythm of one or two calls per second; a monotonous "wee-wee-wee". In contrast to high hooting, which is mostly undirected, the performer always orients to another individual and gives some form of display, usually a rocking or swaying movement in the same rhythm as the vocalization. Teeth-baring is quite common in the middle of the call, but in between calls there is usually no particular expression
Greeting Grunt/Pant grunt	A rhythmic series of brief, grunt-like, vocalized air expulsions sounding like "eh-eh-eh". The grunts are breathy and moderately loud, with an abrupt onset over a broad frequency range, uttered in a rhythm of one or two grunts per second
Panting Laugh	Vocalized, jerky breathing which sounds like coarse low- pitched grunting. Usually it is rather soft, but during wild wrestle bouts it can become quite loud. Similarly to 'greeting grunts', the vocalization is unstructured, covering a broad frequency range. The difference with greeting grunts is in the longer duration and the irregular, accelerating and decelerating, rhythm of the panting laugh. The accompanying facial expression is always a 'play face'.
Pout Moan	Low-pitched, melodious call sounding like a whining "hoo-hoo". No sound spectrogram was collected. The facial expression is always a pout face.
Whistle Bark	A single, loud, high-pitched bark, sometimes sounding like a "wieew"-bark but of shorter duration, 0.05-0.10 sec, and in a shriller voice. Especially in juveniles the bark sounds like a whistle. The whistle-bark may be given with or without baring of the teeth
Food Peep	Soft peeps and high-pitched grunts are the bonobo's most common vocalizations. They are used to draw attention to and "comment" on objects, food, and events in the environment.

	There exists great variation in the sound of these calls, also in the consecutive calls of a single per- former, much of which may be meaningful to the bonobos themselves. No attempt was made, during the present study, to systematically collect data on this vocal behavior as such a task would have interfered with other objectives. Especially during feeding and foraging bonobos utter peeps. The calls are brief, approximately 0.10 sec, clear and tonal, with an average peak frequency in the lowest harmonic of 2.2 kHz. There is no particular facial expression.
Alarm Peep	This call is hard to distinguish by ear from the 'food peep'. It is slightly lower-pitched, with an approximate peak of 1.7 kHz in the lowest harmonic. The alarm peep is also louder and more modulated, almost like a bark, but of the same short duration as the food peep
Peep Yelp	The peep yelp sounds shriller than the other peep sounds, and is of longer duration. It reaches an average pitch of 3.1 kHz in the lowest harmonic and lasts anywhere from 0.05-0.35 sec, with an average of 0.20 sec. The peep yelp is a pure, tonal, relatively unmodulated sound with no or few harmonics in the spectrogram. The facial expression always involves partial or complete teeth-baring with closed mouth.
Scream	This is the bonobo's most intense vocal display. It does not occur without teeth-baring, usually in the form of complete lip-retraction, exposing both teeth and gums. The mouth may be wide open. The shrill and rasping sounds are given at full vocal strength. Compared to other sounds, screams are of long duratin; on the average they last 0.40 sec, and the maximum duration recorded is 1.10 sec. Spectrograms of screams show large numbers of harmonics; the main distinguishing feature of this vocalization. At least four scream types can be distinguished, both acoustically and on the basis of spectrographic analysis: Peep scream: An intermediate between the 'peep yelp' and 'full scream'; the vocalization has the yelp's unmodulated pitch but a less pure, more rasping quality. This vocalization is not a discrete type as the entire spectrum between peep yelps and screams can be heard. Rasp scream: A modulated scream, which sounds hoarser and more rasping than the other scream types. A double-tone may be distinguishable by ear, as if there are two voices in one. Bark scream: Both the beginning and the end of the screams are tonal, the frequency ascending and descending as in a bark. In the middle of this "bark" there is a scream-like part of variable duration, with a shrill rasping timbre. If this part is very brief, the calls may sound like 'staccato hooting'. Bark screams, however, have an average pitch of around 3.3 kHz compared to 2.3 kHz for staccato hooting. Full scream: This is the most typical scream with a full range of harmonics. It is of relatively long duration, and hardly modulated.

Appendix 15 – Persistence/Elaboration and Bonobo Dominance Style

We descriptively examined the relationship between bonobo dominance style components and the ‘Persistence/Elaboration’ measure. As demonstrated in figure A, three of these four relationships are slightly negative, while the remaining one is slightly positive.

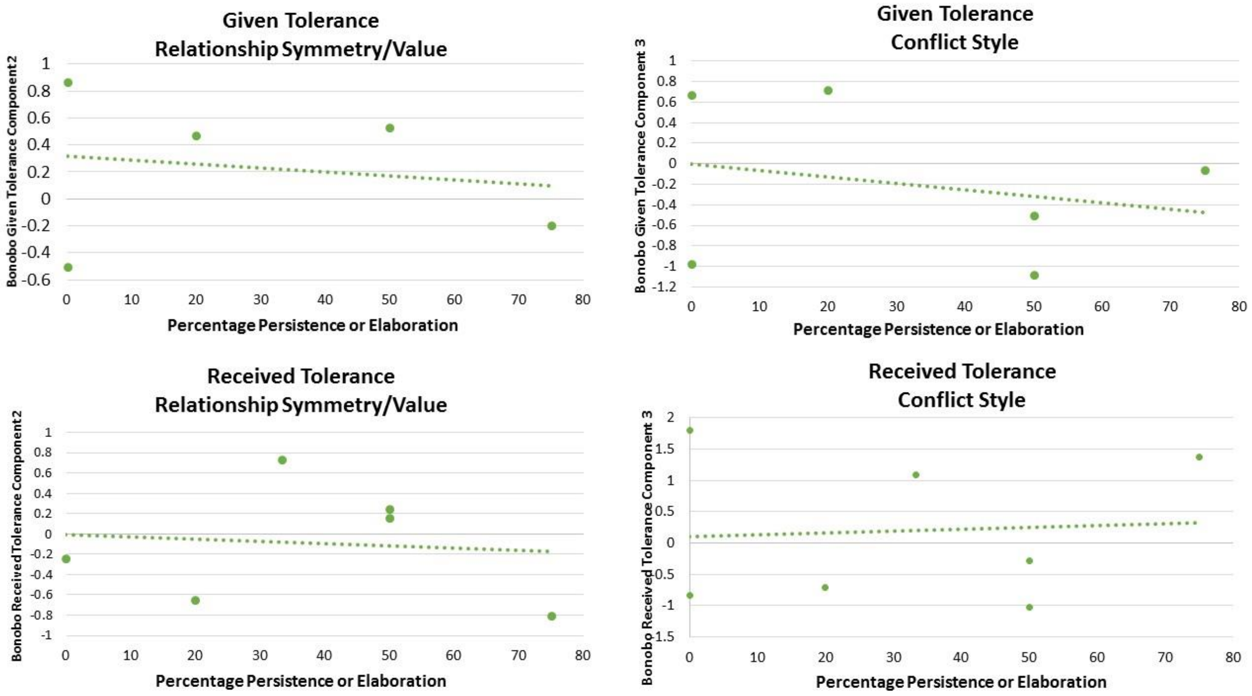


Figure A – Relationships between bonobos’ given and received dominance style components (component 2; relationship symmetry and value, component 3; conflict style) with the persistence/elaboration measure (the percentage of episodes in which the first signal got no response that the signaller persisted or elaborated)

Appendix 16 – Results from models with alternative distributions

We report here additional results to demonstrate that, where an ideal distribution could not be identified, findings are similar across models with alternative distributions,

1. Chimpanzee given tolerance component score and multimodal signals:

   In the main text we reported an LMM with chimpanzee given tolerance component score as the fixed effect, group as a random effect, and proportion of multimodal signals in signal bouts as the outcome variable, and found that this was non-significant. The same model but with log10 transformation on the dependent variable was also non-significant (x^2= 0.811, p= 0.368), as was the equivalent GLMM with a gamma distribution and inverse link (x^2=0.774, p=0.379).

2. Bonobo given tolerance component 2 score and multimodal signal use:

   In the main text we reported an LMM with bonobo given tolerance component 2 score as the fixed effect, group as a random effect, and proportion of multimodal signals in signal bouts as the outcome variable, and found that this was non-significant. The same model but with log10 transformation on the dependent variable was also non-significant (x^2= 0.415, p= 0.519), as was the equivalent GLMM with a gamma distribution and inverse link (x^2=0.270, p=0.600).

3. Bonobo given tolerance component 3 score and multimodal signal use:

   In the main text we reported an LMM with bonobo given tolerance component 3 score as the fixed effect, group as a random effect, and proportion of multimodal signals in signal bouts as the outcome variable, and found that this was non-significant. The same model but with log10 transformation on the dependent variable was also non-significant (x^2= 0.007, p= 0.935), as was the equivalent GLMM with a gamma distribution and inverse link (x^2=0.007, p=0.934).

4. Bonobo received tolerance component 2 score and multimodal signal use:

   In the main text we reported an LMM with bonobo received tolerance component 2 score as the fixed effect, group as a random effect, and proportion of multimodal signals in signal bouts as the outcome variable, and found that this was non-significant. The same model but with log10 transformation on the dependent variable was also non-significant (x^2= 0.989, p= 0.320), as was the equivalent GLMM with a gamma distribution and inverse link (x^2=1.369, p=0.242).

5. Bonobo received tolerance component 3 score and multimodal signal use:

   In the main text we reported an LMM with bonobo received tolerance component 3 score as the fixed effect, group as a random effect, and proportion of multimodal signals in signal bouts as the outcome variable, and found that this was non-significant. The same model but with log10 transformation on the dependent variable was also non-significant (x^2= 1.109, p= 0.292), as was the equivalent GLMM with a gamma distribution and inverse link (x^2=1.845, p=0.174).

6. Bonobo received tolerance component 3 score and sequence use:

   In the main text we reported an LMM with bonobo received tolerance component 3 score as the fixed effect, group as a random effect, and proportion of sequences in signal bouts as the outcome variable, and found that this was non-significant. The same model but with log10 transformation on the dependent variable was also non-significant (x^2= 1.171, p= 0.279), as was the equivalent GLMM with a gamma distribution and inverse link (x^2=1.385, p=0. 239).

References

Alberts, S.C., Hollister-Smith, J.A., Mututua, R., Sayialel, S.N., Muruthi, P.M., Warutere, J.K., Altmann, J., (2005). Seasonality and long term change in a savanna environment. In: Brockman, D.K., Van Schaik, C.P. (Eds.), *Seasonality in Primates: Studies of Living and Extint Human and Non-Human Primates.* Cambridge University Press, Cambridge

Allen, W. (2001). *Green phoenix: Restoring the tropical forests of Guanacaste, Costa Rica.* Oxford University Press, New York.

Altschul, D., Beran, M. J., Bohn, M., Caspar, K., Fichtel, C., Försterling, M., Grebe, N.M., Hernandez-Aguilar, A., Chai Kwok, S., Llorente, M., Motes-Rodrigo, A., Proctor, D., Sánchez-Amaro, A., Simpson, E.A., Scabelska, A., Taylor, D., van der Mescht, J., Völter, C.J., and Watzek, J., (2019). Collaborative open science as a way to reproducibility and new insights in primate cognition research. *Japanese Psychological Review, 62*(3), 205-220.

Archie, E. A., Morrison, T. A., Foley, C. A., Moss, C. J., and Alberts, S. C. (2006). Dominance rank relationships among wild female African elephants, *Loxodonta africana. Animal Behaviour, 71*(1), 117-127.

Arnold, C., L. J. Matthews, and C. L. Nunn. 2010. The 10kTrees Website: A New Online Resource for Primate Phylogeny. *Evolutionary Anthropology 19*:114-118.

Aureli, F., and Schino, G. (2019). Social complexity from within: how individuals experience the structure and organization of their groups. *Behavioral ecology and sociobiology, 73*(1), 6.

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., Connor, R., Di Fiore, A., Dunbar, R., Henzi, S.P., Holekamp, K., Korstjens, A.H., Layton, R., Lee, P., Lehmann, J., Manson, J., Ramos-Fernandez, G., Strier, K., and van Schaik, C. (2008). Fission-fusion dynamics: new research frameworks*. Current Anthropology, 49*(4), 627-654.

Balasubramaniam, K. N., Dittmar, K., Berman, C. M., Butovskaya, M., Cooper, M. A., Majolo, B., Ogawa, H., Schino, G., Thierry, B., and de Waal, F. B. M., (2012). Hierarchical steepness and phylogenetic models: phylogenetic signals in *Macaca*. *Animal Behaviour, 83*(5), 1207-1218.

Balasubramaniam, K. N., Dittmar, K., Berman, C. M., Butovskaya, M., Cooper, M. A., Majolo, B., Ogawa, H., Schino, G., Thierry, B., and de Waal, F. B. M., (2012). Hierarchical steepness, counter-aggression, and macaque social style scale. *American journal of primatology, 74*(10), 915-925.

Barrett, L., Henzi, S. P., and Lusseau, D. (2012). Taking sociality seriously: the structure of multi-dimensional social networks as a source of information for individuals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1599), 2108-2118.

Barton, R. A. (1996). Neocortex Size and Behavioural Ecology in Primates. *Proceedings of the Royal Society B: Biological Sciences, 263*(1367), 173–177.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai., B., Scheipl, F., Grothendieck, G., Green, P., and Fox, J., (2015). Package 'lme4'. *Convergence, 12*(1), 2.

Bergman, T. J., and Beehner, J. C. (2015). Measuring social complexity. *Animal behaviour, 103*, 203-209.

Bergstrom, M. L., and Fedigan, L. M. (2013). Dominance style of female white-faced capuchins. *American Journal of Physical Anthropology, 150*(4), 591–601.

Berman, C. M., Ionica, C. S., and Li, J. (2004). Dominance style among *Macaca thibetana* on Mt. Huangshan, China*. International Journal of Primatology, 25*(6), 1283-1312.

Bermejo, M., and Omedes, A. (1999). Preliminary vocal repertoire and vocal communication of wild bonobos (*Pan paniscus*) at Lilungu (Democratic Republic of Congo). *Folia Primatologica, 70*(6), 328-357.

Bernstein, I. S. (1976). Dominance, aggression and reproduction in primate societies. *Journal of Theoretical Biology, 60*(2), 459-472.

Bernstein, I. S. (1981). Dominance: The baby and the bathwater. *Behavioral and brain sciences, 4*(3), 419-429.

Blanca, M., Alarcón, R., Arnau, J., Bono, R., and Bendayan, R. (2017). Non-normal data: Is ANOVA still a valid option? *Psicothema, 29*(4), 552-557.

Blumstein DT, Armitage KB (1997) Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. *Am Nat 150*:179–200.

Boehm, (1999*). Hierarchy in the forest: The evolution of egalitarian behavior.* Harvard University Press.

Boesch, C. (2009). *The real chimpanzee: sex strategies in the forest*. Evolutionary Anthropology. Cambridge University Press.

Bouchet, H., Blois-Heulin, C., and Lemasson, A. (2013). Social complexity parallels vocal complexity: a comparison of three non-human primate species. *Frontiers in Psychology, 4*, 390.

Briseño-Jaramillo, M., Biquand, V., Estrada, A., and Lemasson, A. (2017). Vocal repertoire of free-ranging black howler monkeys' (*Alouatta pigra*): call types, contexts, and sex-related contributions. *American journal of primatology, 79*(5), e22630.

Brown, C. H., and Waser, P. M. (1988). Environmental influences on the structure of primate vocalizations. In: *Primate vocal communication* (pp. 51-66). Springer, Berlin, Heidelberg.

Brown, C. H., Gomez, R., and Waser, P. M. (1995). Old world monkey vocalizations: adaptation to the local habitat? *Animal Behaviour, 50*(4), 945-961.

Burt, A. (1989). Comparative methods using phylogenetically independent contrasts. *Oxford surveys in evolutionary biology, 6,* 33-53.

Byrne, R. W., Cartmill, E., Genty, E., Graham, K. E., Hobaiter, C., and Tanner, J. (2017). Great ape gestures: intentional communication with a rich set of innate signals. *Animal cognition, 20*(4), 755-769.

Candiotti, A., Zuberbühler, K., and Lemasson, A. (2012). Context-related call combinations in female Diana monkeys. *Animal Cognition, 15(*3), 327-339.

Canli, T., and Lesch, K.-P. (2007). Long story short: the serotonin transporter in emotion regulation and social cognition. *Nature Neuroscience, 10*(9), 1103–1109.

Carne, C., Wiper, S., and Semple, S. (2011). Reciprocation and interchange of grooming, agonistic support, feeding tolerance, and aggression in semi-free-ranging Barbary macaques. *American Journal of Primatology, 73*(11), 1127-1133.

Cartmill, E. A., and Byrne, R. W. (2011). Addressing the problems of intentionality and granularity in non-human primate gesture. *Integrating gestures: the interdisciplinary nature of gesture* (eds G. Stam and M. Ishino), Amsterdam, The Netherlands: John Benjamins.

Castles, D. L., Aureli, F., and de Waal, F. B. (1996). Variation in conciliatory tendency and relationship quality across groups of pigtail macaques. *Animal Behaviour, 52*(2), 389-403.

Clarke, A. S., and Boinski, S. (1995). Temperament in nonhuman primates. *American Journal of Primatology, 37*(2), 103–125.

Clay, Z., and Zuberbühler, K. (2011). Bonobos extract meaning from call sequences. *PLoS One, 6*(4).

Clutton-Brock, T., and Janson, C. (2012). Primate socioecology at the crossroads: Past, present, and future. *Evolutionary Anthropology, 21*(4), 136–150.

Cords, M. (1997). Friendships, alliances, reciprocity and repair. In A.Whiten and R.Byrne (Eds). *Machiavellian intelligence II,* (pp. 24-49). Cambridge University Press.

Cords, M., and Thurnheer, S. (1993). Reconciling with valuable partners by long-tailed macaques. *Ethology, 93*(4), 315-325.

Crockford, C., and Boesch, C. (2005). Call combinations in wild chimpanzees. Behaviour, 397-421.De Waal, F. B. (1988). The communicative repertoire of captive bonobos (Pan paniscus), compared to that of chimpanzees. *Behaviour, 106*(3-4), 183-251.

Crockford, C., Wittig, R. M., Langergraber, K., Ziegler, T. E., Zuberbühler, K., and Deschner, T. (2013). Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B: Biological Sciences, 280*(1755), 20122765.

Cronin, K. A., De Groot, E., and Stevens, J. M. G. (2015). Bonobos Show Limited Social Tolerance in a Group Setting: A Comparison with Chimpanzees and a Test of the Relational Model. *Folia Primatologica,* 164–177.

Cronin, K. A., Van Leeuwen, E. J., Vreeman, V., and Haun, D. B. (2014). Population-level variability in the social climates of four chimpanzee societies. *Evolution and Human Behavior, 35*(5), 389-396.

De Marco, A., Rebout, N., Massiot, E., Sanna, A., Sterck, E. H., Langermans, J. A. Cozzolini, R., Thierry, B., and Lemasson, A. (2019). Differential patterns of vocal similarity in tolerant and intolerant macaques. *Behaviour, 1*(aop), 1-25.

De Vries, H. (1995). An improved test of linearity in dominance hierarchies containing unknown or tied relationships. *Animal Behaviour, 50*(5), 1375-1389.

de Vries, H., Stevens, J. M., and Vervaecke, H. (2006). Measuring and testing the steepness of dominance hierarchies. *Animal Behaviour, 71*(3), 585-592.

de Waal, F.B., (1977). The organization of agonistic relations within two captive groups of Java-monkeys (*Macaca fascicularis). Zeitschrift für Tierpsychologie, 44(*3), 225-282.

de Waal, F.B., (1986). Class structure in a rhesus monkey group: the interplay between dominance and tolerance. *Animal Behaviour, 34*(4), 1033-1040.

de Waal, F.B., (1988). The communicative repertoire of captive bonobos (Pan paniscus), compared to that of chimpanzees. *Behaviour, 106*(3-4), 183-251.

de Waal, F.B., (1989). Dominance "style" and primate social organisation. In: StadenV, FoleyRA, editors*. Comparative socioecology.* Oxford: Blackwell. p 243–263

de Waal, F.B., (1991). Rank distance as a central feature of rhesus monkey social organization: a sociometric analysis. *Animal Behaviour, 41*(3), 383-395.

de Waal, F.B., and Johanowicz, D. L., Development, C., and Jun, N. (1993). Modification of Reconciliation Behavior Through Social Experience : An Experiment with Two Macaque Species Modification of Reconciliation Behavior through Social Experience : An Experiment with Two Macaque Species. *Child Development, 64*(3), 897–908.

de Waal, F.B., and Lanting, F. (1997). *Bonobo: The forgotten ape.* Univ of California Press.

de Waal, F.B., and Luttrell L.M. (1985). The formal hierarchy of rhesus macaques: an investigation of the bared-teeth display. *Am J Primatol 9*:73–85.

de Waal, F.B., and Luttrell, L. M. (1989). Toward a Comparative Socioecology of the Genus Macaca: Different Dominance Styles in Rhesus and Stumptail Monkeys. *American Journal of Primatology, 19,* 83–109.

Deaner, R. O., and Nunn, C. L. (1999). How quickly do brains catch up with bodies? A comparative method for detecting evolutionary lag. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 266*(1420), 687-694.

Demuru, E., Ferrari, P. F., and Palagi, E. (2015). Emotionality and intentionality in bonobo playful communication. *Animal Cognition, 18*(1), 333-344.

Dobson, S. D. (2012). Coevolution of facial expression and social tolerance in macaques. *American Journal of Primatology, 74*(3), 229-235.

Drews, C. (1993). The concept and definition of dominance in animal behaviour. *Behaviour*, *125*(3-4), 283-313.

Dunbar, R. (1998). *Grooming, gossip, and the evolution of language.* Harvard University Press.

Dunbar, R. (1998). The social brain hypothesis *Evol. Anthropol., 6,* 178–190.

Dunbar, R. I. (1992). Neocortex size as a constraint on group size in primates*. Journal of human evolution, 22*(6), 469-493.

Dunbar, R. I. (1993). Coevolution of neocortical size, group size and language in humans. *Behavioral and brain sciences, 16*(4), 681-694.

Dunn, J. C., and Smaers, J. B. (2018). Neural Correlates of Vocal Repertoire in Primates*. Frontiers in Neuroscience, 12*, 534.

Eisenberg, J. F. (1976). Communication mechanisms and social integration in the black spider monkey, *Ateles fusciceps robustus*, and related species. *Smithsonian contributions to zoology*.

Ekman, R. (1997). *What the face reveals: Basic and applied studies of spontaneous expression using the Facial Action Coding System (FACS)*. Oxford University Press, USA.

Ey, E., Rahn, C., Hammerschmidt, K., and Fischer, J. (2009). Wild female olive baboons adapt their grunt vocalizations to environmental conditions. *Ethology, 115*(5), 493-503.

Faraut, L., Siviter, H., Dal Pesco, F., and Fischer, J. (2019). How life in a tolerant society affects the usage of grunts: evidence from female and male Guinea baboons. *Animal Behaviour, 153*, 83-93.

Fedigan L. 1993. Sex differences and intersexual relations in adult white-faced capuchins (*Cebus capucinus*). *Int J Primatol* 14:853–877.

Fedurek, P., and Slocombe, K. E. (2011). Primate vocal communication: a useful tool for understanding human speech and language evolution? *Human Biology, 83*(2), 153-174.

Field, A. (2013). *Discovering statistics using IBM SPSS statistics.* Sage.

Fischer, A., Prüfer, K., Good, J. M., Halbwax, M., Wiebe, V., André, C., Atencia, R., Mugisha, L., Ptak, S.E., Pääbo, S. (2011). Bonobos fall within the genomic variation of Chimpanzees. *PLoS ONE, 6*(6), e21605.

Fischer, J., and Hammerschmidt, K. (2002). An overview of the Barbary macaque, Macaca sylvanus, vocal repertoire. *Folia Primatologica, 73*(1), 32-45.

Fischer, J., Farnworth, M. S., Sennhenn-Reulen, H., and Hammerschmidt, K. (2017). Quantifying social complexity. *Animal Behaviour, 130*, 57-66.

Fischer, J., Farnworth, M. S., Sennhenn-Reulen, H., and Hammerschmidt, K. (2017). Quantifying social complexity. *Animal Behaviour, 130,* 57-66.

Fischer, J., Wadewitz, P., and Hammerschmidt, K. (2017). Structural variability and communicative complexity in acoustic communication. *Animal behaviour, 134,* 229-237.

Fitch, W. T. (2005). The evolution of language: a comparative review. *Biology and philosophy, 20*(2-3), 193-203.

Flack, J.C.F., and de Waal, F.B.D. (2004). Dominance style-social power and conflict management: a conceptual framework. *Macaque societies: A model for the study of social organization*, *41*, 157.

Fleiss, J. L. (1981). Balanced incomplete block designs for inter-rater reliability studies. *Applied Psychological Measurement*, *5*(1), 105-112.

Fortunato, M. (2009). Dominance Style in Captive, Fission-fusioned Bonobos (Pan paniscus): Dominance Hierarchy, Aggressive Patterns, and Conflict Management. PhD Dissertation.

Foster, M. W., Gilby, I. C., Murray, C. M., Johnson, A., Wroblewski, E. E., and Pusey, A. E. (2009). Alpha male chimpanzee grooming patterns: implications for dominance "style". *American Journal of Primatology: Official Journal of the American Society of Primatologists, 71*(2), 136-144.

Fowler, A., and Hohmann, G. (2010). Cannibalism in wild bonobos (*Pan paniscus*) at Lui Kotale. *American Journal of Primatology, 72*(6), 509–514.

Fraser, O. N., and Aureli, F. (2008). Reconciliation, consolation and postconflict behavioral specificity in chimpanzees. *American Journal of Primatology, 70*(12), 1114–1123.

Freckleton, R. P., Harvey, P. H., and Pagel, M. (2002). Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist, 160*(6), 712-726.

Freeberg, T. M., Dunbar, R. I., and Ord, T. J. (2012). Social complexity as a proximate and ultimate factor in communicative complexity. *Philosophical Transactions of the Royal Society, 367,* 1785-1801.

Fröhlich, M., and van Schaik, C. P. (2018). The function of primate multimodal communication. *Animal cognition, 21*(5), 619-629.

Fruth, B., and Hohmann, G. (2003). Intra- and Inter-Sexual Aggression By Bonobos in the Context of Mating. *Behaviour, 140*(11), 1389–1413.

Fruth B, Hickey JR, Andre C, Furuichi T, Hart J, Hart T, Kuehl H, Maisels F, Nackoney J, Reinartz G, Sop T, Thompson J and Williamson EA (2016) *Pan paniscus*. The IUCN Red List Assessment of Threatened Species, version 3.1. IUCN.

Furuichi, T. (1997). Agonistic interactions and matrifocal dominance rank of wild bonobos (*Pan paniscus*) at Wamba. *International Journal of Primatology, 18*(6), 855-875.

Furuichi, T. (2011). Female contributions to the peaceful nature of bonobo society. *Evolutionary Anthropology: Issues, News, and Reviews*, *20*(4), 131-142.

Galinsky, A. D., Magee, J. C., Inesi, M. E., and Gruenfeld, D. H. (2006). Power and perspectives not taken. *Psychological science, 17*(12), 1068-1074.

Gamba, M., Friard, O., Riondato, I., Righini, R., Colombo, C., Miaretsoa, L., Torti, V., Nadhourou, B., and Giacoma, C. (2015). Comparative analysis of the vocal repertoire of Eulemur: a dynamic time warping approach. *International Journal of Primatology, 36*(5), 894-910.

Genty, E., Neumann, C., and Zuberbühler, K. (2015). Complex patterns of signalling to convey different social goals of sex in bonobos, *Pan paniscus*. *Scientific reports, 5*(1), 1-13.

Ghazanfar, A. A., and Hauser, M. D. (1999). The neuroethology of primate vocal communication: substrates for the evolution of speech. *Trends in cognitive sciences, 3*(10), 377-384.

Goodall, J. (1986). *The chimps of Gombe: Patterns of behavior.* Cambridge University Press.

Grafen, A. (1989). The phylogenetic regression. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences, 326*(1233), 119-157.

Graham, K. E., Furuichi, T., and Byrne, R. W. (2017). The gestural repertoire of the wild bonobo (*Pan paniscus*): a mutually understood communication system. *Animal cognition, 20*(2), 171-177.

Green, S. (1975). Variation of vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*): a field study. *Primate behavior*, 1-102.

Gros-Louis, J. J., Perry, S. E., Fichtel, C., Wikberg, E., Gilkenson, H., Wofsy, S., and Fuentes, A. (2008). Vocal repertoire of *Cebus capucinus*: acoustic structure, context, and usage. *International Journal of Primatology, 29*(3), 641-670.

Gruber, T., and Clay, Z. (2016). A comparison between bonobos and chimpanzees: A review and update. Evolutionary Anthropology: Issues, News, and Reviews, 25(5), 239-252.

Gruber, T., Clay, Z., and Zuberbühler, K. (2010). A comparison of bonobo and chimpanzee tool use: evidence for a female bias in the Pan lineage. *Animal Behaviour, 80*(6), 1023-1033.

Grunau, T., and Kuester, J. (2001). Dominance style in female guerezas (*Colobus guereza*). *Primates, 42*(4), 301-307.

Gustison, M. L., le Roux, A., and Bergman, T. J. (2012). Derived vocalizations of geladas (*Theropithecus gelada*) and the evolution of vocal complexity in primates. *Philosophical Transactions of the Royal Society B: Biological Sciences, 367*(1597), 1847-1859.

Gustison, M. L., Semple, S., Ferrer-i-Cancho, R., and Bergman, T. J. (2016). Gelada vocal sequences follow Menzerath's linguistic law*. Proceedings of the National Academy of Sciences, 113*(19), E2750-E2758.

Hadfield, J. D. (2010) 'MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package', *Journal of Statistical Software, 33*(2), pp. 1–22.

Hadfield, J. D., and Nakagawa, S. (2010). General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of evolutionary biology, 23*(3), 494-508.

Hamilton, W. D. (1971). Geometry for the selfish herd*. Journal of Theoretical Biology, 31*(2), 295–311.

Hammerschmidt, K., and Fischer, J. (1998). The vocal repertoire of Barbary macaques: a quantitative analysis of a graded signal system*. Ethology, 104*(3), 203-216.

Hammerschmidt, K., and Fischer, J. (2019). Baboon vocal repertoires and the evolution of primate vocal diversity*. Journal of human evolution, 126,* 1-13.

Harcourt, A. H., Hauser, M., and Stewart, K. J. (1993). Functions of wild gorilla 'close' calls: Repertoire, context, and interspecific comparison*. Behaviour, 124*(1-2), 89-122.

Hare, B., and Kwetuenda, S. (2010). Bonobos voluntarily share their own food with others. *Current Biology, 20*(5), R230-R231.

Hare, B., Melis, A. P., Woods, V., Hastings, S., and Wrangham, R. (2007). Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology, 17*(7), 619-623.

Hare, B., Wobber, V., and Wrangham, R. (2012). The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. *Animal Behaviour, 83*(3), 573-585.

Hauser, M. D. (1993). The evolution of nonhuman primate vocalizations: effects of phylogeny, body weight, and social context. *The American Naturalist, 142*(3), 528-542.

Heesen, R., Hobaiter, C., Ferrer-i-Cancho, R., and Semple, S. (2019). Linguistic laws in chimpanzee gestural communication*. Proceedings of the Royal Society B, 286*(1896), 20182900.

Hemelrijk, C. K. (1999). An individual-orientated model of the emergence of despotic and egalitarian societies. *Proceedings of the Royal Society B: Biological Sciences, 266*(1417), 361–369.

Higham, J. P., and Hebets, E. A. (2013). An introduction to multimodal communication. *Behavioral Ecology and Sociobiology, 67*(9), 1381-1388.

Higley, J. D., Suomi, S. J., and Chaffin, A. C. (2011). Impulsivity and aggression as personality traits in nonhuman primates. *Personality and Temperament in Nonhuman Primates,* 257–283.

Hobaiter, C., and Byrne, R. W. (2011). Serial gesturing by wild chimpanzees: its nature and function for communication. *Animal cognition, 14*(6), 827-838.

Hobaiter, C., and Byrne, R. W. (2011). The gestural repertoire of the wild chimpanzee. *Animal cognition, 14*(5), 745-767.

Hobaiter, C., and Byrne, R. W. (2014). The meanings of chimpanzee gestures. *Current Biology, 24(*14), 1596-1600.

Hohmann, G. (1989). Vocal communication of wild bonnet macaques (*Macaca radiata*). *Primates, 30*(3), 325-345.

Hopkins, W. D., Taglialatela, J. P., and Leavens, D. A. (2011). Do chimpanzees have voluntary control of their facial expressions and vocalizations. *Primate communication and human language: Vocalisation, gestures, imitation and deixis in humans and non-humans,* 1, 71-88.

Horn, J. L. (1965). A rationale and test for the number of factors In factor analysis. *Psychometrika, 30*, 179-185.

Humle, T., Maisels, F., Oates, J. F., Plumptre, A., and Williamson, E. A. (2016). *Pan troglodytes.* The IUCN Red List Assessment of Threatened Species, version 3.1

Humphrey, N. K. (1976). The social function of intellect. In *Growing points in ethology* (pp. 303-317). Cambridge University Press.

Ihobe, H., and Furuichi, T. (1994). Variation in Male Relationships in Bonobos and Chimpanzees. *Behaviour, 130*(3), 211–228.

Jaeggi, A. V., Stevens, J. M. G., and Van Schaik, C. P. (2010). Tolerant food sharing and reciprocity is precluded by despotism among bonobos but not chimpanzees. *American Journal of Physical Anthropology, 143*(1), 41–51.

Janecke, B. B. 2002. Vegetation ecology of Soetdoring Nature Reserve: Pan, grassland, and karroid communities (MSc thesis). Bloemfontein, South Africa: University of the Free State.

Joly, M., Micheletta, J., De Marco, A., Langermans, J. A., Sterck, E. H., and Waller, B. M. (2017). Comparing physical and social cognitive skills in macaque species with different degrees of social tolerance. *Proceedings of the Royal Society B: Biological Sciences, 284(*1862), 20162738.

Kaewpanus, K., (2014). Behavior and vocal communication of Assamese macaque (*macaca assamensis*) At Tham Pla temple, Chiang Rai province. (Unpublished doctoral thesis). Chiang Mai University, Chiang Mai, Thailand.

Kappeler, P. M. (2019). A framework for studying social complexity. *Behavioral ecology and sociobiology*, *73*(1), 13.

Kelley, T. L. (1927). *Interpretation of educational measurements.* New York: Macmillan.

Koenig, A., and Borries, C. (2009). The lost dream of ecological determinism: Time to say goodbye? ... Or a white Queen's proposal? *Evolutionary Anthropology, 18*(5), 166–174.

Koski, S. E., and Sterck, E. H. M. (2007). Triadic postconflict affiliation in captive chimpanzees: does consolation console? *Animal Behaviour, 73*(1), 133–142.

Koski, S.E., Koops, K. and Sterck, E. (2007). Reconciliation, Relationship Quality, and Postconflict Anxiety: Testing the Integrated Hypothesis in Captive Chimpanzees. *American Journal of Primatology, 69*, 158–172.

Kottek et al., 2006, World map of the Köppen-Geiger climate classification updated, *Meteorologische Zeitschrift,* 15, 259-263

Kudo, H. (1987). The study of vocal communication of wild mandrills in Cameroon in relation to their social structure. *Primates, 28*(3), 289-308.

Kutsukake, N., and Castles, D. L. (2004). Reconciliation and post-conflict third-party affiliation among wild chimpanzees in the Mahale Mountains, Tanzania. *Primates, 45*(3), 157–165.

Langergraber, K. E., Prufer, K., Rowney, C., Boesch, C., Crockford, C., Fawcett, K., … Vigilant, L. (2012). Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution*. Proceedings of the National Academy of Sciences, 109*(39), 15716–15721.

Leavens, D. A., Russell, J. L., and Hopkins, W. D. (2005). Intentionality as measured in the persistence and elaboration of communication by chimpanzees (*Pan troglodytes*). *Child Development, 76*(1), 291-306.

Lehmann J, Majolo B, McFarland R (2016) The effects of social network position on the survival of wild Barbary macaques, *Macaca sylvanus. Behav Ecol 27*:20–28

Lehmann, J., and Boesch, C. (2009). Sociality of the dispersing sex: the nature of social bonds in West African female chimpanzees*, Pan troglodytes. Animal Behaviour, 77*(2), 377-387.

Lemasson, A., and Hausberger, M. (2011). Acoustic variability and social significance of calls in female Campbell's monkeys (*Cercopithecus campbelli campbelli*). *The Journal of the Acoustical Society of America, 129*(5), 3341-3352.

Lemasson, A., Ouattara, K., Petit, E. J., and Zuberbühler, K. (2011). Social learning of vocal structure in a nonhuman primate? *Evolutionary Biology, 11*(1), 362.

Lewis, R. J. (2002). Beyond dominance: the importance of leverage. *The Quarterly review of biology, 77*(2), 149-164.

Liebal, K., Call, J., and Tomasello, M. (2004). Use of gesture sequences in chimpanzees. *American Journal of Primatology: Official Journal of the American Society of Primatologists, 64*(4), 377-396.

Liebal, K., Waller, B. M., Slocombe, K. E., and Burrows, A. M. (2014). *Primate communication: a multimodal approach.* Cambridge University Press.

Macedonia, J. M. (1993). The vocal repertoire of the ringtailed lemur (Lemur catta). *Folia primatologica, 61*(4), 186-217.

Maciej, P., Ndao, I., Hammerschmidt, K., and Fischer, J. (2013). Vocal communication in a complex multi-level society: constrained acoustic structure and flexible call usage in Guinea baboons. *Frontiers in zoology, 10*(1), 58.

Maestripieri, D. (1999). Primate social organization, gestural repertoire size, and communication dynamics: a comparative study of macaques. *The evolution of language: Assessing the evidence from nonhuman primates.*

Maestripieri, D. (2005). Gestural communication in three species of macaques (Macaca mulatta, M. nemestrina, M. arctoides): use of signals in relation to dominance and social context. *Gesture, 5*(1), 57-73.

Maestripieri, Dario (1999). Primate social organization, gestural repertoire size, and communication dynamics: A comparative study of macaques. In Barbara J. King (Ed.), *The origins of language: What nonhuman primates can tell us (*pp. 55–77). Santa Fe, NM: The School of American Research.

Maretti, G., Sorrentino, V., Finomana, A., Gamba, M., and Giacoma, C. (2010). Not just a pretty song: an overview of the vocal repertoire of Indri indri. *Journal of anthropological sciences,* Rivista di antropologia: JASS, 88, 151-165.

Marler, P. (1961). The logical analysis of animal communication. *Journal of theoretical biology, 1*(3), 295-317.

Marler, P. (1973). A Comparison of Vocalizations of Red-tailed Monkeys and Blue Monkeys, *Cercopithecus ascanius* and *C. mitis*, in Uganda 1. *Zeitschrift für Tierpsychologie, 33*(3-4), 223-247.

Matsumura, S. (1999). The evolution of “egalitarian” and “despotic” social systems among macaques. *Primates, 40*(1), 23-31.

Matsumura, S., and Kobayashi, T. (1998). A game model for dominance relations among group-living animals. *Behavioral Ecology and Sociobiology*, *42*(2), 77-84.

McComb, K., and Semple, S. (2005). Coevolution of vocal communication and sociality in primates. *Biology letters, 1*(4), 381-385.

Meese, G. B., and Ewbank, R. (1973). The establishment and nature of the dominance hierarchy in the domesticated pig. *Animal Behaviour, 21*(2), 326-334.

Melin A.D., Young H.C., Mosdossy K.N., Fedigan L.M., (2014). Seasonality, extractive foraging and the evolution of primate sensorimotor intelligence*. J Hum Evol* 71:77–86.

Morbeck, M. E., and Zihlman, A. L. (1989). Body size and proportions in chimpanzees, with special reference to *Pan troglodytes schweinfurthii* from Gombe National Park, Tanzania. *Primates, 30*(3), 369-382

Muller, M. N., Kahlenberg, S. M. and Wrangham, R. W. 2009. Male aggression against females and sexual coercion in chimpanzees. In: *Sexual Coercion in Primates and Humans* (Ed. by M. N. Muller and R. W. Wrangham), pp. 184e217. London: Harvard University Press.

Newton-Fisher, N. E. (2004). Hierarchy and social status in Budongo chimpanzees. *Primates, 45*(2), 81-87.

Noë, R., de Waal, F. B. M., and van Hooff, J. A. R. A. M. (1980). Types of dominance in a chimpanzee colony. *Folia Primatol. 34*: 90–110.

Orme, D., Freckleton, R., Thomas, G., and Petzoldt, T. (2013). The caper package: comparative analysis of phylogenetics and evolution in R. *R package version, 5*(2), 1-36.

Owings, D. H., and Morton, E. S. (1998). *Animal vocal communication: a new approach*. Cambridge University

Pagel, M. (1994). Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters*. Proceedings of the Royal Society of London. Series B: Biological Sciences, 255*(1342), 37-45.

Palagi, E., Cordoni, G., and Tarli, S. B. (2006). Possible roles of consolation in captive chimpanzees (*Pan troglodytes). American Journal of Physical Anthropology, 129*(1), 105–111.

Palagi, E., Paoli, T., and Tarli, S. B. (2004). Reconciliation and Consolation in Captive Bonobos (*Pan paniscus). American Journal of Primatology, 62*(1), 15–30.

Panggur, R.P. (2014). Vocal communication of wild crested macaques. (Unpublished doctoral thesis). Graduate School Institut Pertanian Bogor, Bogor, Indonesia.

Parish, A. R. (1996). Female relationships in bonobos (*Pan paniscus*) - Evidence for bonding, cooperation, and female dominance in a male-philopatric species*. Hu Nat, 7*(1), 61–96.

Parish, A. R., De Waal, F. B., and Haig, D. (2000). The other “closest living relative”: How bonobos (*Pan paniscus*) challenge traditional assumptions about females, dominance, intra-and intersexual interactions, and hominid evolution. *Annals of the New York Academy of Sciences, 907*(1), 97-113.

Parr, L. A., Waller, B. M., Vick, S. J., and Bard, K. A. (2007). Classifying chimpanzee facial expressions using muscle action*. Emotion, 7*(1), 172.

Partan, S. R., and Marler, P. (2005). Issues in the classification of multimodal communication signals. The American Naturalist, 166(2), 231-245.

Partan, S. R., and Marler, P. (2005). Issues in the classification of multimodal communication signals. *The American Naturalist, 166*(2), 231-245.

Partan, S. R., Larco, C. P., and Owens, M. J. (2009). Wild tree squirrels respond with multisensory enhancement to conspecific robot alarm behaviour. *Animal Behaviour, 77*(5), 1127-1135.

Partan, S., and Marler, P. (1999). Communication goes multimodal. *Science, 283,* 1272-1273

Patzelt, A., Pirow, R., and Fischer, J. (2009). Post-conflict affiliation in Barbary macaques is influenced by conflict characteristics and relationship quality, but does not diminish short-term renewed aggression. *Ethology,* 115(7), 658-670.

Peckre, L., Kappeler, P. M., and Fichtel, C. (2019). Clarifying and expanding the social complexity hypothesis for communicative complexity. *Behavioral ecology and sociobiology, 73*(1), 11.

Petersdorf, M., Weyher, A. H., Kamilar, J. M., Dubuc, C., and Higham, J. P. (2019). Sexual selection in the Kinda baboon. *Journal of human evolution,* 135, 102635.

Piper, W. H. (1997). Social dominance in birds. In *Current ornithology* (pp. 125-187). Springer, Boston, MA.

Pollick, A. S., and De Waal, F. B. (2007). Ape gestures and language evolution. *Proceedings of the National Academy of Sciences, 104*(19), 8184-8189.

Preuschoft S. (1999). Are primates behaviorists? Formal dominance, cognition, and freefloating rationales. *J Comp Psychol 113*: 91–95.

Preuschoft, S., and van Hooff, J. A. (1995). Homologizing primate facial displays: A critical review of methods. *Folia Primatologica, 65*(3), 121-137.

Preuschoft, S., and van Schaik, C. P. (2000). Dominance and communication. Conflict management in various social settings, 77-105.

Preuschoft, S., Wang, X., Aureli, F., and De Waal, F. B. M. (2002). Reconciliation in Captive Chimpanzees: A Reevaluation with Controlled Methods*. International Journal of Primatology, 23*(1).

Ramos-Fernandez, G., King, A. J., Beehner, J. C., Bergman, T. J., Crofoot, M. C., Di Fiore, A., Lehmann, J., Schaffner, C.M., Snyder-Mackler, N., Zuberbuhler. K., Aureli, F., and Boyer, D., (2018). Quantifying uncertainty due to fission–fusion dynamics as a component of social complexity. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1879), 20180532.

Range, F., and Fischer, J. (2004). Vocal repertoire of sooty mangabeys (*Cercocebus torquatus atys*) in the Taï National Park. *Ethology, 110*(4), 301-321.

Revelle, W. (2015). Procedures for personality and psychological research. *Northwestern University, Evanston, IL*.

Rowe N. Pogonias (1996). *The pictorial guide to the living primates.* New York.

RStudio Team (2015). RStudio: Integrated Development for R. RStudio, Inc., Boston, MA URL http://www.rstudio.com/.

Salmi, R., Hammerschmidt, K., and Doran-Sheehy, D. M. (2013). Western gorilla vocal repertoire and contextual use of vocalizations. *Ethology, 119*(10), 831-847.

Schel, A. M., Townsend, S. W., Machanda, Z., Zuberbühler, K., and Slocombe, K. E. (2013). Chimpanzee alarm call production meets key criteria for intentionality. *PloS one, 8(*10).

Schino, G. (2001). Grooming, competition and social rank among female primates: a meta-analysis. *Animal Behaviour, 62*(2), 265-271.

Semple, S., Hsu, M. J., and Agoramoorthy, G. (2010). Efficiency of coding in macaque vocal communication. *Biology Letters, 6*(4), 469-471.

Seyfarth, R. M. (1977). A model of social grooming among adult female monkeys. *Journal of theoretical Biology, 65*(4), 671-698.

Seyfarth, R. M., Cheney, D. L., and Marler, P. (1980). Monkey responses to three different alarm calls: evidence of predator classification and semantic communication. *Science, 210*(4471), 801-803.

Shultz, S., and Dunbar, R. I., (2007). The evolution of the social brain: anthropoid primates contrast with other vertebrates. *Proceedings of the Royal Society B: Biological Sciences, 274*(1624), 2429–2436.

Silk J, Cheney D, Seyfarth R (2013) A practical guide to the study of social relationships. *Evol Anthropol Issues News Rev,* 22:213–225

Silk, J.B., Roberts, E.R., Städele, V., Strum, S.C. (2018). To grunt or not to grunt: Factors governing call production in female olive baboons, *Papio Anubis. PLoS One, 13* (11).

Silk, J.B., Seyfarth, R.M., and Cheney, D.L. (2016). Strategic use of affiliative vocalizations by wild female baboons. *PLoS One, 11* (10).

Slocombe, K. E., and Zuberbühler, K. (2005). Functionally referential communication in a chimpanzee. *Current Biology, 15*(19), 1779-1784.

Slocombe, K. E., and Zuberbühler, K. (2010). Vocal communication in chimpanzees. *The mind of the chimpanzee: ecological and experimental perspectives.* University of Chicago, Chicago, 192-207.

Slocombe, K. E., and K. Zuberbuhler. (2005). Agonistic screams in wild chimpanzees (*Pan troglodytes schweinfurthii*) vary as a function of social role*. J. Comp. Psychol. 119*:67–77.

Slocombe, K. E., Waller, B. M., and Liebal, K. (2011). The language void: the need for multimodality in primate communication research*. Animal Behaviour, 81*(5), 919-924.

Smith, C. L., and Evans, C. S. (2013). A new heuristic for capturing the complexity of multimodal signals. *Behavioral Ecology and Sociobiology, 67*(9), 1389-1398.

Smith, W. J. (1977). *The behavior of communicating: an ethological approach*. Harvard University Press, Cambridge, MA

Sol, D., Maspons, J., Vall-Llosera, M., Bartomeus, I., García-Peña, G. E., Piñol, J., and Freckleton, R. P. (2012). Unraveling the life history of successful invaders*. Science, 337*(6094), 580-583.

Stanford, C. B. (1998). The social behavior of chimpanzees and bonobos: empirical evidence and shifting assumptions. *Current anthropology, 39*(4), 399-420.

Stephan, C., and Zuberbühler, K. (2014). Predation affects alarm call usage in female Diana monkeys (*Cercopithecus diana diana*). *Behavioral ecology and sociobiology, 68(*2), 321-331.

Stephan, C., and Zuberbühler, K. (2016). Social familiarity affects Diana monkey (*Cercopithecus diana diana*) alarm call responses in habitat-specific ways. *Royal Society open science, 3*(2), 150639.

Stevens, J. M. G., Vervaecke, H., De Vries, H., and Van Elsacker, L. (2007). Sex differences in the steepness of dominance hierarchies in captive bonobo groups*. International Journal of Primatology, 28(*6), 1417–1430.

Strushaker, T. T. (1967). Auditory communication among vervet monkeys (*Cercopithecus aethiops*) in SA Altmann, ed., *Social Communication among Primates*.

Tan, J., and Hare, B. (2013). Bonobos share with strangers. *PLoS One, 8*(1), e51922.

Thierry, B. (1990). L'état d'équilibre entre comportements agonistiques chez un groupe de macaques japonais (*Macaca fuscata*). *Comptes Rendus de l'Académie des Sciences de Paris*, Series III, 310.

Thierry, B. (2000). Management Patterns across Macaque Species. *Natural conflict resolution,* 106.

Thierry, B. (2007). Unity in diversity: lessons from macaque societies*. Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews, 16*(6), 224-238.

Thierry, B. (2008). Primate socioecology, the lost dream of ecological determinism. *Evolutionary Anthropology, 17*(2), 93–96.

Thierry, B. (2013). Identifying constraints in the evolution of primate societies. *Philosophical Transactions of the Royal Society B: Biological Sciences, 368(*1618)

Thierry, B., Anderson, J. R., Demaria, C., Desportes, C., and Petit, O. (1994). Tonkean macaque behaviour from the perspective of the evolution of Sulawesi macaques. In *Current Primatology Social Development, 2, 103*–117.

Thierry, B., Aureli, F., Nunn, C. L., Petit, O., Abegg, C., and de Waal, F. B. M. (2008). A comparative study of conflict resolution in macaques: insights into the nature of trait covariation. Animal *Behaviour, 75(*3), 847–860.

Thierry, B., Iwaniuk, A. N., and Pellis, S. M. (1999). The Infuence of Phylogeny on the Social Behaviour of Macaques. *Ethology, 106*, 602–617

Thierry, B., Singh, M., and Kaumanns, W. (2004). *Macaque Societies: A Model for the Study of Social Organization.* New York Cambridge University Press (Vol. 1).

Tokuyama, N., and Furuichi, T. (2016). Do friends help each other? Patterns of female coalition formation in wild bonobos at Wamba. *Animal Behaviour, 119*, 27-35.

Tomasello M, Call J, Nagell, K, Olguin R, Carpenter M. (1994). The learning and the use of gestural signals by young chimpanzees: a trans-generational study*. Primates 35*:137–154.

Tomasello, M. and Zuberbühler, K. (2002). Primate vocal and gestural communication. In: *The Cognitive Animal: Empirical and Theoretical Perspectives on Animal Cognitio*n (Ed. by M. Bekoff, C. S. Allen and G. Burghardt), pp. 293e299. Cambridge, Massachusetts: MIT Press.

Treves, A. (1999). Has predation shaped the social systems of arboreal primates?. *International Journal of Primatology, 20*(1), 35-67.

van Schaik, C. (1989). The Ecology of Social Relationships Amongst Female Primates. Comparative Socioecology: *The Behavioural Ecology of Humans and Other Mammals*, 195–218.

Van Schaik, C. P. (1983). Why Are Diurnal Primates Living in Groups? *Behaviour, 87*(1), 120–144

Velicer, W. F. (1977). An Empirical Comparison Of The Similarity Of Principal Component, Image, And Factor Patterns. *Multivariate Behavioral Research, 12*(1), 3-22.

Vervaecke, H., de Vries, H., and Van Elsacker, L. (2000a). Dominance and its behavioral measures in a captive group of bonobos (*Pan paniscus). International Journal of Primatology, 21*, 47–68.

Wadewitz, P., Hammerschmidt, K., Battaglia, D., Witt, A., Wolf, F., and Fischer, J. (2015). Characterizing vocal repertoires—Hard vs. soft classification approaches. *PloS one, 10*(4), e0125785.

Waller, B. M., Liebal, K., Burrows, A. M., and Slocombe, K. E. (2013). How can a multimodal approach to primate communication help us understand the evolution of communication? *Evolutionary Psychology, 11*(3).

Weiss, A., Adams, M. J., Widdig, A., and Gerald, M. S. (2011). Rhesus macaques (*Macaca mulatta*) as living fossils of hominoid personality and subjective well-being. *J Comp Psychol, 125,* 72-83.

Weiss, A., King, J. E., and Perkins, L. (2006). Personality and subjective well-being in orang-utans (*Pongo pygmaeus* and *Pongo abelii*). *Journal of Personality and Social Psychology*, 90, 501-511.

Welch, B. L. (1951). On the comparison of several mean values: an alternative approach. *Biometrika, 38*(3-4), 330-336.

Whitehead, H. 2009. SOCPROG programs: analyzing animal social structures. *Behavioral Ecology and Sociobiology 63:* 765-778.

Whiten, A., and Arnold, K. (2001). Post-Conflict Behaviour of Wild Chimpanzees (Pan Troglodytes Schweinfurthii) in the Budongo Forest, Uganda*. Behaviour, 138*(5), 649–690.

Whiten, A., and Byrne, R. W. (Eds.). (1997). *Machiavellian intelligence II: Extensions and evaluations* (Vol. 2). Cambridge University Press.

Wilke, C., Kavanagh, E., Donnellan, E., Waller, B. M., Machanda, Z. P., and Slocombe, K. E. (2017). Production of and responses to unimodal and multimodal signals in wild chimpanzees, *Pan troglodytes schweinfurthii. Animal Behaviour, 123,* 305-316.

Wilkins, M. R., Seddon, N., and Safran, R. J. (2013). Evolutionary divergence in acoustic signals: causes and consequences. *Trends in ecology and evolution, 28*(3), 156-166.

Wilson, M. L., Boesch, C., Fruth, B., Furuichi, T., Gilby, I. C., Hashimoto, C., Hobaiter, C., Hohmann, G., Itoh, N., Koops, K., Lloyd, J., Matzuzawa, T., Mitani, J., Mjungu, D., Morgan, D., Muller, M., Mundry, R., Nakamuru, M., Pruetz, J., Pusey, A., Riedel, J., Sanz, C., Schel, A., Simmons, N., Waller, M., Watts, D., White, F., Wittig, R., Zuberbuhler, K., and Wrangham, R. (2014). Lethal aggression in Pan is better explained by adaptive strategies than human impacts. *Nature, 513(*7518), 414.

Wittig, R. M., and Boesch, C. (2003). Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park*. International Journal of Primatology, 24*(4), 847–867.

Wrangham, R. W. (1999). Evolution of coalitionary killing. *American journal of physical anthropology, 110*(S29), 1-30.

Zhang, P., and Watanabe, K. (2014). Intraspecies variation in dominance style of Macaca fuscata. *Primates, 55*(1), 69-79.

Kano, T. (1992). *The last ape: Pygmy chimpanzee behavior and ecology.* Stanford University Press.

Zuberbühler, K. (2005). The phylogenetic roots of language: evidence from primate communication and cognition. *Current Directions in Psychological Science, 14*(3), 126-130.